ILLINOIS BIOLOGICAL MONOGRAPHS

PUBLISHED QUARTERLY
UNDER THE AUSPICES OF THE GRADUATE SCHOOL
BY THE UNIVERSITY OF ILLINOIS

VOLUME IV

Urbana, Illinois
1918-1919

34881

EDITORIAL COMMITTEE

STEPHEN ALFRED FORBES WILLIAM TRELEASE

HENRY BALDWIN WARD

TABLE OF CONTENTS

VOLUME IV

NUMBERS		PAGES
1	Life History Studies on Montana Trematodes. By Ernest Carroll Faust. With 9 plates and one text figure	1-120
	(Distributed March 6, 1918)	
2	The Goldfish (*Carassius carassius*) as a Test Animal in the Study of Toxicity. By Edwin B. Powers. With graphs and tables	121-194
	(Distributed July 28, 1918)	
3	Morphology and Biology of Some Turbellaria from the Mississippi Basin. By Ruth Higley With 3 plates	195-288
	(Distributed December 31, 1918)	
4	North American Pseudophyllidean Cestodes from Fishes. By Arthur Reuben Cooper. With 13 plates	288-542
	(Distributed May 31, 1919)	

ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. IV July, 1917 No. 1

EDITORIAL COMMITTEE

STEPHEN ALFRED FORBES WILLIAM TRELEASE

HENRY BALDWIN WARD

PUBLISHED UNDER THE
AUSPICES OF THE GRADUATE SCHOOL BY
THE UNIVERSITY OF ILLINOIS

COPYRIGHT BY THE UNIVERSITY OF ILLINOIS 1918
DISTRIBUTED MARCH 6, 1918

LIFE HISTORY STUDIES ON MONTANA TREMATODES

WITH 9 PLATES AND
1 TEXT FIGURE

BY
ERNEST CARROLL FAUST

Contributions from the
Zoological Laboratory of the University of Illinois
under the direction of Henry B. Ward, No. 98

THESIS

SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN ZOOLOGY IN THE GRADUATE SCHOOL OF THE UNIVERSITY OF ILLINOIS

1917

TABLE OF CONTENTS

	Pages
Introduction	7
Methods of Investigation	7
Biology of the Bitter Root Valley	9
Morphology of Trematodes Found	13
Introduction	13
Embryology	14
Parthenitae (Sporocyst and Redia)	18
Cercaria General	23
Integument	27
Parenchyma	29
Musculature	30
Armature	31
Glands	32
Excretory System	36
Digestive System	43
Genital System	44
Nervous System	47
Description of the Trematodes Infecting Mollusks of the Bitter Root Valley	57
Introduction	57
Monostomata	58
Cercaria pellucida Faust 1917	58
Cercaria konadensis Faust 1917	61
Holostomata	62
Cercaria flabelliformis Faust 1917	62
Tetracotyle pipientis nov. spec	64
Cercaria ptychocheilus Faust 1917	66
Distomata	68
Xiphidiocercariae	68
Cercaria crenata Faust 1917	68
Cercaria glandulosa Faust 1917	69
Cercaria diaphana Faust 1917	71
Cercaria dendritica Faust 1917	72
Cercaria micropharynx Faust 1917	74
Cercaria racemosa Faust 1917	75
Echinostome Cercariae	76
Cercaria trisolenata Faust 1917	76
Cercaria biflexa Faust 1917	78
Furcocercariae	80
Cercaria gracillima Faust 1917	80
Cercaria tuberistoma Faust 1917	82
Pathology	84
Problems Presented	86
Interrelation of Trematodes	86
Relation of Trematodes to Other Groups	90
Life Cycle of the Digenetic Trematodes	92
Summary	94
Species Described in this Paper	95
Bibliography	96
Explanation of Plates	102

INTRODUCTION

During a two years' residence at Missoula, Montana, from 1914 to 1916 the writer became acquainted with the biology of the inter-mountain region of the Bitter Root valley. The heavy trematode infection of the animals in this locality has led to an investigation of the life history of the trematodes of the region.

An opportunity is taken at this place to express appreciation to all who have aided in this study, but especially to Professor Henry B. Ward whose kindness and sincere interest have made the work possible.

METHODS OF INVESTIGATION

This study is confined to the trematodes infecting mollusks. The majority of the collections were made by Mr. Norbert Sager of Missoula. A sketch map (text-fig. 1) indicates the location of each collection. The snails were shipped in damp green moss and arrived in excellent condition.

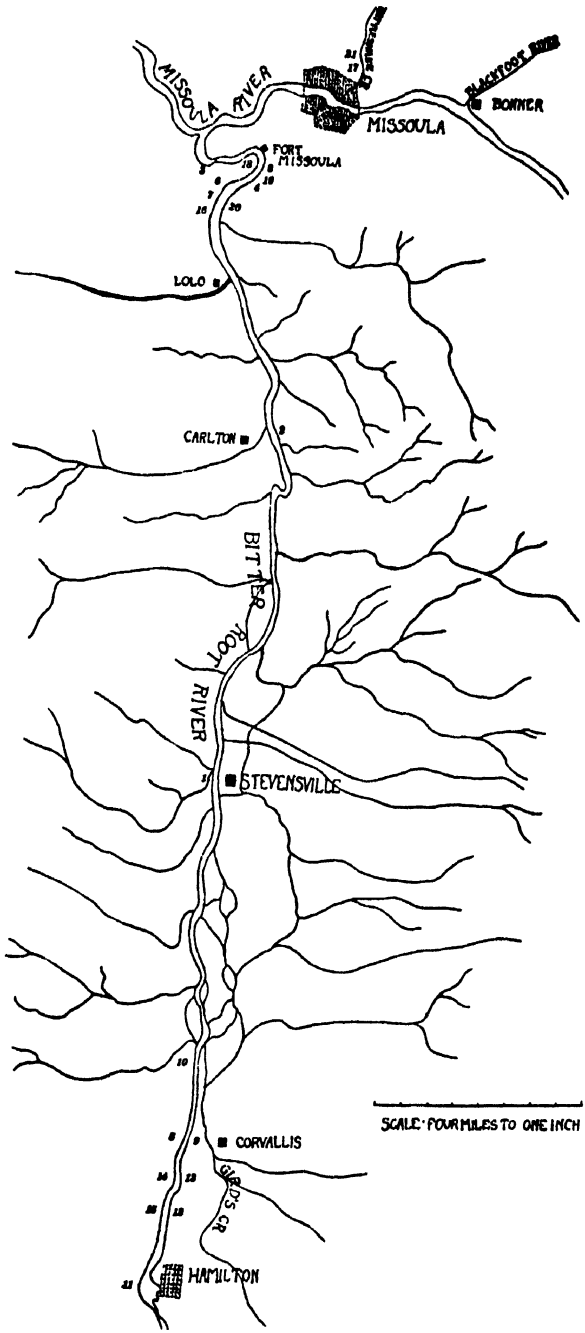
These observations on living material gave data on the stages of development within the mollusk, on the methods of locomotion, on encystment, and on the excretory system.

The worms were removed from the infected tissue and placed in a watch glass in 0.3 per cent saline solution. The change from the host tissue to the saline medium usually caused rapid movement.

It is essential that the excretory system be studied in the living material as, aside from the vesicle and the main trunks of this system, very little can be made out in the preserved material. The delicate structure of the flame cells and the finer capillaries makes it necessary that these organs be examined in living specimens, for in fixation they are likely to collapse, even with the most careful technic.

The organs of the digestive system come out equally well in living and preserved mounts. Some systems, as a rule, can be made out only from preserved and stained material. The most important of these is the genital complex. For all ordinary purposes the material was fixed in Gilson's reagent, altho equally good results were obtained from a corrosive-acetic fixing agent. From the preserved material toto mounts and sections were made, using Delafield's hematoxylin and Ehrlich's acid hematoxylin as stains. A strong counter-stain of eosin in the sections brought out remarkably well the nerve fibers of the worms. Wax models were made of the mature and immature stages of the nervous system of cercariae and parthenitae.

Care was taken to keep the mounts acid-free, and for that purpose all reagents except the destaining fluid were made slightly alkaline with dessicated



Text-figure 1. Sketch map of the Bitter Root Valley, Montana, showing localities where collections were made.

potassium acetate. Some specimens were fixed without any acid fraction in the reagent in order to preserve the excretory granules. These granules, as well as the mucoid cyst membrane of the encysted worm, gave beautiful biuret and xanthoproteic reactions, suggesting a tyrosine compound.

BIOLOGY OF THE BITTER ROOT VALLEY

The snails commonly found in the Bitter Root valley are *Physa gyrina* Say, *Lymnaea proxima* Lea, and *Planorbis trivolvis* Say. They have been identified by Mr. Bryant Walker of Detroit, Michigan. All of these snails were collected from the lower part of the valley, but *Planorbis trivolvis* was not found in the upper reaches of the river. These mollusks are the hosts of the trematodes considered in this paper.

Two facts stand out predominantly in the study of these parasites: the large number of species of trematodes in the snails in the limited range of the valley, and the high per cent of infection both among individuals of a species and within the individual of the species.

There have been found in a single season's collection thirteen trematode species in the snails of the valley, and one larval trematode in the squaw-fish, *Ptychocheilus oregonensis* Richardson. A total of fifteen collections of snails was made during the fall of 1916 and four collections during May 1917. Seventeen of these collections contained trematode infection. *Lymnaea proxima* was taken eight times from five different localities, *Physa gyrina* was taken eleven times from eight different localities, and *Planorbis trivolvis* was taken three times from two localities (Table I, see next page).

The infection record shows that the host is not specific. In the infection of mollusks with *Cercaria pellucida* the host around Buckhouse Bridge was Physa, while that up the valley was Lymnaea. *Cercaria gracillima* was found both in Physa and in Lymnaea in the region of Buckhouse Bridge from different collections. *Cercaria trisolenata* was found both in Physa and in Lymnaea in the region of Buckhouse Bridge and in the vicinity of Fort Missoula. While no parasite species was found in more than two of the three snails common in the valley, there is reason to believe that the third species of snail might be the host under proper conditions. This view is contrasted with that of Thomas (1883:106) who found that only one English mollusk, *Lymnaea trunculata*, "could serve as an intermediate host to the liver fluke," altho this writer suggested that other species of snails must serve in other countries as hosts to the worm This preference for a particular mollusk in a particular locality, coupled with the ability to select a different molluscan host in another locality, has been found to hold true not only for *Fasciola hepatica*, but also for *Schistosoma haematobium* (Leiper, 1916) and *S. mansoni* (Leiper, 1916; Lutz, 1916; Iturbe and Gonzalez, 1917). When two hosts so different structurally as Physa and Planorbis are equally heavily infected, it seems evident that the stimulus to which the miracidium of the fluke responds can

TABLE I

DISTRIBUTION OF CERCARIAE IN THE BITTER ROOT VALLEY

SPECIES	Stevensville	Carlton	Maclay Sloughs	Fort Sloughs	Corvallis	Buckhouse Bridge	Buckhouse Bridge	Fort Springs	Corvallis	2 mi. below Corvallis	5 mi above Corvallis	3 mi above Corvallis	1½ mi. above Corvallis	1½ mi above Corvallis	3 mi above Corvallis	Roadhouse	Rattlesnake Creek	Fort Sloughs	Fort Springs	Buckhouse Bridge	Rattlesnake Creek
	NUMBER OF COLLECTION																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Monostomes																					
Cercaria pellucida						a							b								
C. konadensis													b								
Holostomes																					
C. flabelliformis					a				a	a											
C ptychocheilus	d	d																			
Distomes																					
C crenata							b														
C glandulosa											a										
C diaphana													b								
C dendritica				b			b														
C micropharynx																	b				b
C racemosa							b														
C trisolenata			a		a	a												b	b		
			c			c															
C. biflexa																a				c	
C gracillima			a			a	b									a	b	b		a	
C tuberistoma												a									

a, Physa gyrina b, Lymnaea proxima c, Planorbis trivolvis d, Ptychocheilus oregonensis
Compare with map on page 8

not be specific. In the case of *Cercaria trisolenata*, where the infection ranged from 22 to 100 per cent in Physa and from 50 to 100 per cent in Planorbis, the host must be considered facultative.

In several instances the same species of snail from the same collection harbored two or more cercariae (cf. collections nos 3, 6, 7, 13, 16, 17, 18). For example (Table I), at the Maclay Sloughs both *Cercaria trisolenata* and *C. gracillima* were found in the same host species, Physa, in fact in the same individual. This case is paralleled by the record of Cort (1915:55), where the sporocysts of *Cercaria polyadena* and *C. reflexae* were found within the same liver tissue of *Lymnaea reflexa*. However, Ssinitzin (1911) in an examination of several thousand snails of six species, in which he discovered twenty-one species of cercariae, makes no record of two species in the same host individual.

In the collection of *Lymnaea proxima* from Buckhouse Bridge three species of trematodes were found as parasites, *Cercaria dendritica*, *C. racemosa*, and

C. gracillima. In such a case as this, one species, *C. dendritica*, was present in each host in large numbers, while *C. racemosa* was less frequent, and the third species of worm, *C. gracillima*, constituted a very light infection in only one of the thirty-two snails examined Hausmann (1897:16) in referring to the dominance of one parasite species in the individual host, regards this phenomenon as a biological antagonism.

Turning to the per cent of infection in the snails collected in the fall of 1916 (Table II), a heavy parasitism is found to exist The data are especially significant when compared with the records of other investigators. Cort (1915) gives detailed data for eleven species of mollusks collected from nine localities. His collections were made in the fall of 1913. The least per cent of individuals infected was 1 4, that for *Pleurocerca elevatum*, secured from the Sangamon River at Mahomet, Illinois This mollusk contained *Cercaria megalura*. The heaviest infection recorded by Cort was that with *C. isocotylea*, where an 18 per cent infection was found in *Planorbis trivolvis* from Urbana, Illinois. The average infection from Cort's eleven species records is 8.5 per cent Ssinitzin (1911) has recorded data from twenty-one species of cercariae described by him for the vicinity of the Black Sea at Sebastopol. In many cases his records show a uniquely low parasitism, practically insignificant from a pathological point of view. Out of 1159 individuals of *Rissoa venusta* he

TABLE II

INFECTION RECORD FOR CERCARIAE OF THE BITTER ROOT VALLEY

	SPECIES	HOST	EXAMINED	INFECTED	PER CENT
1	Cercaria pellucida	a	18	1	5 5
2	Cercaria pellucida	b	16	5	31 3
3	Cercaria lonadensis	b	16	5	31 3
4	Cercaria flabelliformis	a	34	5	14 7
5	Cercaria flabelliformis	a	10	3	30 0
6	Cercaria flabelliformis	a	12	3	25 0
7.	Cercaria ptychocheilus	d	6	6	100 0
8	Cercaria crenata	b	22	3	13 6
9	Cercaria glandulosa	a	5	2	40 0
10	Cercaria diaphana	b	16	5	31 3
11	Cercaria dendritica	b	14	5	35 7
12	Cercaria dendritica	b	29	3	10 3
13.	Cercaria microparynx	b	32	18	56 3
14	Cercaria racemosa	b	29	3	10 3
15	Cercaria trisolenata	a	12	12	100 0
16	Cercaria trisolenata	c	1	1	100 0
17.	Cercaria trisolenata	a	8	2	25 0
18.	Cercaria trisolenata	a	18	4	22 2
19.	Cercaria trisolenata	c	2	1	50 0
20.	Cercaria biflexa	a	71	5	7 0
21	Cercaria gracillima	a	12	1	8 3
22	Cercaria gracillima	a	18	1	5 5
23.	Cercaria gracillima	a	29	5	17 3
24.	Cercaria gracillima	a	71	33	46.5
25.	Cercaria gracillima	b	32	1	3.1
26.	Cercaria tuberistoma	a	19	1	5.3

a, Physa gyrina b, Lymnaea proxima c, Planorbis trivolvis d, Ptychocheilus oregonensis

found only one was infected with *Cercaria cribrata* and one with *C. metentera*, or, in each case, only a 0.06 per cent infection. The heaviest infection found by Ssinitzin among these twenty-one species of parasites was that of *C. zernowi* in *Cardium exiguum*, 7.0 per cent. The average for the twenty-one species is only 1.34 per cent. In the cases of the worms found in *Cerithiolum exile* and *Rissoa venusta*, the percentage of infection is so low that no parasites would have been found had not a large number of snails been collected and examined. The record of Iturbe and Gonzalez (1917) for the cercariae of *Schistosoma mansoni* in Venezuela shows a heavy infection.

The infection in mollusks of the Bitter Root valley is decidedly heavy, altho it varies within wide limits under different factors of place and season. The lowest percentage of infection found was that with *Cercaria gracillima* in *Lymnaea proxima* at Buckhouse Bridge, 3.1. From a different slough in the same locality one month later a 46.5 per cent infection with this species was found in Physa. Thus the percentage of infection is found to fluctuate within a very circumscribed area. The least infection of Physa with *C. gracillima* was from the Maclay Sloughs farther down the River, 5.5 per cent. On the other hand, *C. trisolenata* was found as a hundred per cent infection in both Physa and Planorbis collected from these same sloughs. Taken as a whole the infection average during the fall of 1916 for the Bitter Root mollusks is 29.02 per cent. The average by host species is somewhat different, 24.8 per cent for Lymnaea, 25.16 per cent for Physa, and 75.0 per cent for Planorbis. Leaving Planorbis out of consideration because of the few specimens collected there is an average infection of over 24 per cent in Lymnaea and in Physa. The per cent infection for May 1917 (not included in table II) gives an average of 11.5 for Lymnaea, 16.6 for Physa, and 50.0 for Planorbis.

MORPHOLOGY OF TREMATODES

INTRODUCTION

The progress in the morphological and histological knowledge of larval trematodes is wrapped up in the development of discriminate observation and interpretation on the part of investigators. This has been aided in no small degree by the use of better technic and by better optical equipment, but it is for the most part the observer's own expectation that differences must exist in larvae, and his determination to discover faithfully and accurately such a differentiation of structure, that has brought about progress in this line of investigation. No clearer conception of the change in point of view can be obtained than by a contrast of the statement of La Valette, a worker in the field six decades ago, with the expression of Charles Sedgwick Minot just ten years ago. In his Symbolae ad Trematodum Evolutionis Historiam La Valette (1855:34) recites: "nonnullae Trematodum larvae tam exiguam offerunt differentiam ut discrimina earum characteristica vix commonstari queant." Minot (1897:928) voices the modern point of view in his declaration that "it is not true that all embryos are alike; on the contrary they show class, ordinal, and generic differences from one another."

While the writer fully agrees with the idea that the most natural way of correlating larval trematodes with the adult forms is by a knowledge of their life histories, yet such a correlation is not always possible. Looss (1896) probably had the cercaria of *Schistosoma haematobium* among some of the furcocercariae that came under his observation, yet he was forced to admit (p. 167) that "tous ces efforts ont été, quant a la *Bilharzia* complètement négatifs." The writer has attacked this part of the problem with the idea in mind that not only the fundaments of the adult trematode are found in the mature cercaria, but that even the main descriptive features of the adult trematode are already present, so that the worker can recognize the adult in the larva. While it has been impossible to show species correlations between larva and adult it has been found in the course of the investigation that the larva shows clearly the family features that hitherto have been inferred only by the "blunderbuss method" of life-history investigations.

Probably none of the adult trematodes genetically related to the larvae studied have been described. Moreover, the characters common both to larva and adult have been overlooked in the study of many adult species. The writer has been confronted with the problem as to what characters of the larva are ephemeral and what ones are common to cercaria and adult trematode. A thoro analysis of the groups studied, including Monostomata, Holostomata, and Distomata, gives convincing proof that the most constant systems in larva and adult are the nervous, genital and excretory systems. Such systems and organs as tail, cystogenous glands, and stylet are distinctly larval in nature and may or may not show the same relationship as the natural grouping based on characters common to both larva and adult.

EMBRYOLOGY

"Larval trematode" has been used for any phase of the life-history from the fertilized egg to the adult trematode. This is truly a wrong conception in the light of the observations of investigators from early times down to the present. Workers have recognized sporocyst and redia as "nurse" to the progeny. In other words, they are parthenogenetic individuals. Ssinitzin (1905, 1910, 1911) has made a wise separation of sporocyst and redia on the one hand from the cercaria on the other. He groups the mature sporocyst and redia together under the term *parthenita*, or parthenogenetic mother. This term is used thruout this paper to define the mature sporocyst and redia as distinguished from cercaria or other larval trematode of the hermaphroditic generation.

The homology between cercaria, sporocyst and redia in their early stages of development is recognized by Schwarze (1886:64), who compares his studies on the cercaria's development with those of Schauinsland (1883) on miracidia. Schwarze notes the similarity of the "cuticula," the sloughing off of the epidermis, the location of the solid entoblast, which divides so that a portion comes to lie next to the ectoderm and another part around the gut. He shows that the homology is very apparent. "Die Keimzellen des Embryos entsprechen den Genitalzellen der Cercarie, die etwas abgeplatteten Epithelzellen des Embryo den Meristemzellen der Cercarie." He observes the similarity of the excretory system in miracidia, redia and cercaria, and adds "ferner sind sie ebenfalls mit einem Nervensystem ausgestattet, welches die grösste Aehnlichkeit mit demjenigen der Cercarien hat."

Since the miracidium, redia, and cercaria are not, in last analysis, three parts of one life-history, but more exactly three or more genetically related but complete life-histories, it would not be too much to expect, then, that the origin of germ layers in miracidium, redia, and cercaria would be the same. All three generations arise by the cleavage and development of a single germ cell of mesodermal origin. In the miracidium the cell is always fertilized; in the redia and cercaria it is always parthenogenetic. The observations on the similarity of origin of these cells are extensive, yet mostly isolated, and deserve re-emphasis.

The exact method of development of individuals within the sporocyst or redia has been a matter of diversity of opinion. In general one of two views, budding or parthenogenesis, has been supported by investigators. The earlier writers who considered the origin of the germ balls described them as arising endogenously. Thus Moulinié (1856:132) writes: "les Cercaires naissent, comme nous l'avons vu en parlant des Sporocystes, de gemmes plus ou moins arrondis qui se forment dans l'intérieur de ses derniers lorsqu' ils atteint leur développement normal." Then the question arose whether or not the germ ball arose from the ordinary tissues lining the body cavity of sporocyst or redia, or whether special cells were set apart as a germinal epithelium. Leuckart (1886:113-125) asserts that in all cases germ balls arise only from

those cells which remain unquestionably embryonic. He distinquishes between the condition in rediae and sporocysts, for in the former he found a specialized germinal epithelium, while in the latter all of the cells of the body wall remain undifferentiated in character, and in consequence are capable of germ cell production.

Thomas (1883:119) found for the sporocyst-redia generation of *Fasciola hepatica* that the germ balls which develop into rediae arise in part from germinal cells already present in the embryo (sporocyst), but that "they gain an increase in their numbers by the proliferation of cells lining the body cavity." In the rediae he asserts (p. 125) that the majority of the embryos seem to be formed from the transformation of cells at the posterior end. Cells from the body wall become enlarged, and each of these cells undergoes segmentation, giving rise to a morula. Looss (1892:156, 157) is definitely committed to the view that any portion of the epithelium lining the body cavity is capable of producing germ balls, but, as a matter of fact, only the posterior end (the vegetative end) performs such service. Later in the same paper (p. 167) he speaks of the developmental stages as a metamorphosis composed of several generations, in no sense comparable to parthenogenesis. Haswell (1903:500, 501) describes for the sporocyst of an echinostome larva the development of embryos from a single ovarian mass at the posterior end of the body.

Within more recent years the problem of the origin of germ balls has been centered around the criterion of the formation of polar bodies. Coe (1896: 562) found no polar bodies in the germinal epithelium of the sporocyst and redia of *Fasciola hepatica*. Because Reuss (1903:470) found three small granular bodies attached to the germ balls of *Distomum duplicatum* sporocysts, he concluded that maturation occurred. Tennent's work on *Bucephalus haimaenus* (1906:649) supports the argument in favor of the origin of the germ cell from the walls of the body cavity. After the germ cell passes into the body cavity a "polar body" is cut off. Later Tennent has found that there are three cells in the proximity of the germ cell, two of which seem to be the result of division of the first cell. Rossbach (1906:433) finds no cells which he is willing to call polar bodies. He concludes 1) that the small cells near the epithelium are not polar bodies because their walls are not found in direct continuity with the germ cells; 2) that the cells called polar bodies by Reuss are normally present during development of the germ ball, in miracidia, in sporocysts, in rediae, and even in the ovary of sexually mature trematodes; 3) that they are more abundant in the younger sporocysts and rediae, and 4) that they are present in larger numbers than three's. Finally Cary (1909), in his study of the germ cells of an amphistome sporocyst, has found that the germ balls arise from cells of the body wall which mature without reduction and throw off one polar body.

The contribution to the problem of the meaning of the proliferation of germ balls as described in this paper, is based on the development of the germ cells in the rediae of the holostome, *Cercaria flabelliformis* Faust 1917. In the

anterior part of the mother rediae large germ balls of both rediae and cercariae are present. The germinal epithelium is confined to the posterior fourth of the wall lining the body cavity. In some of the larval rediae within the mother rediae the earlier stages of the history of the germ cells have been studied. This has enabled the writer to secure a series of stages of the germ cells all the way from the probable derivation of the mesoderm tissue from the base of the gut up thru maturation and segmentation.

At a stage in the development of the redia when the archenteron is represented by about eight or ten large vesicular cells (Fig. 45), certain cells are found wandering out from the blind end of the gut and spreading thru the body cavity. Some of these cells come to lie against the wall of the cavity and at first appear as protrusions of the wall; later they seem to constitute a loosely formed inner layer of the wall. Other cells of this type are found free in the body cavity. The majority of these cells that have wandered out from the base of the gut are oval in shape, and have attached to them on one side a small, nodular protrusion, consisting of the film of cytoplasm around a densely granular nucleus.

All of these cells, whether attached to the body wall or not, are to be regarded as germ cells, based on their present structure and future behavior. The small nodules are polar bodies. Figure 46 *H* shows this body in process of formation. The mitotic figure is in the anaphase stage, and was found in a germ cell free in the body cavity of a young daughter redia. These data on the origin of the germ cells from the specialized germinal mass at the blind end of the gut support the thesis of Leuckart (1886:123) and Schwarze (1886: 48, 49), that the cells have preserved their original embryonic character. The fact that the production of the polar body and consequent maturation of the germ cells takes place in cells next to the body cavity as well as in those free in the body cavity, explains the observations of Thomas (1883:115) that some of the cells from which the germ balls are derived are "the germinal cells of the embryo or cells derived from them by division, others are formed by a proliferation of the epithelium lining the cavity of the sporocyst," since these two groups are traceable back to a common origin at the base of the gut.

A description is now given in support of the view that the germ cell is a true ovum. In its unmodified condition the germ cell is moderately inconspicuous, similar in all respects to an undifferentiated parenchyma cell. As it begins to change, the cell enlarges, the cytoplasm becomes granular, with many interstitial vacuoles, and the nucleus comes to have a clearly outlined membrane wall. Frequently the chromatin material is massed into a karyosome (Fig. 46 *A*). The chromatin mass now becomes oblong (*B*) and after considerable growth becomes coiled into a thick skein (*C*). The next stage (*D*) shows the division of the skein into eight chromosomes. These chromosomes arrange themselves in an equatorial plate, and soon show a longitudinal splitting. One of these (*b*) is precocious in its behaviour. It wanders toward the edge of the nucleus and divides (b_1, b_2) while the other seven chromosomes

remain with their halves still in contact. The precocious chromosomes take up positions toward the poles of the cell (*G*). The other chromosomes then divide and migrate to opposite poles (*H*), one of these daughter groups being constricted off as a polar body (*I*). As a result of this process eight chromosomes separate by longitudinal splitting, so that half of each goes into the polar body and half remains in the cell. The polar-body remains in cytoplasmic connection with the ovum while the latter undergoes another division. As in the previous division, simple mitosis occurs. The chromosomes b_1, b_2 precede the others in separation into component halves ((*Fig.* 46 *I*). In a late anaphase of this second division (*J*) the polar body may divide, altho this is not always the case.

This second division is not a part of the maturation, for that has been accomplished by the expulsion of the single polar body: hence, it constitutes the first division of the mature ovum. After this (*K*) the polar body is entirely separated from the blastomeres (*L*) and disintegrates. Thus maturation consists of a single mitotic division with the extrusion of a polar body, and takes place without any reduction of chromosomes. In other words, the process is one of true parthenogenesis.

The somatic chromosome count of the developing germ ball is eight, consisting of seven ordinary chromosomes and the precocious individual. In support of this statement is the count of each of the first two blastomeres (*K*, *L*), and the chromosome complex in the late metaphase of an endoderm cell of a morula (*M*). In the latter the count is double, e.g., sixteen, in view of the previous splitting of the chromosomes antecedent to separation into the daughter chromosome groups. The consistent tendency of the chromosome *b* and its descendents to separate from the chromosome mass and to divide before the other seven split, suggests the possibility that this chromosome is a heterosome, two of which Lindner (1914) has found in the adults of *Schistosoma haematobium*.

In the case of the germ balls that never reach the body wall, the process of maturation takes place free in the body cavity. For those cells which lodge against the wall and even fuse with the wall, the process of maturation and cleavage into two blastomeres takes place while the ovum is still in contact with the body wall. At this time it is set free and allowed to develop into a germ ball.

In the older mature rediae (Fig. 44) the epithelial layer of the body wall lining the body cavity consists of a syncytium in which nuclei are arranged irregularly. The cell boundaries become distinct only as maturation of the cells approaches.

Leuckart (1886:124) has stated that it is relatively long after germ ball formation before it is evident whether the embryo is to develop into a redia or cercaria. While the chromosomal history in the rediae of *Cercaria flabelliformis* shows no difference between cells which develop into daughter rediae or cercariae, the cytoplasmic history of this species is indicative of the generation

of the offspring at an early date. The cytoplasm of the germ cells which develop into rediae is granular altho quite transparent. It stains a delicate lavender with Delafield's hematoxylin. On the other hand, from the very outset the cytoplasm of the cercaria type of cell is fibrillar, with many large intermediate vacuoles. It stains a deep magenta with the same dye in the same section as the rediae ova. Figure 46 *L* represents the first cleavage of the cercaria embryo. The chromosome count is identical to that in each blastomere in a redia-forming embryo. Subsequent divisions are difficult to follow on account of the opacity of the cercaria germ-balls. It is very evident, nevertheless, that differentiation of layers and organs takes place much more rapidly in the cercaria ovum than in the redia ovum.

The arguments produced by Rossbach (1906:433), to show that there are no polar bodies given off by the germ cell, do not hold in the case of *Cercaria flabelliformis*. The polar bodies have been found not only in cytoplasmic continuity with the ovum, but in the actual state of mitosis preceding the separation of the polar nucleus from the germ ball. Polar bodies are indeed more numerous in the young rediae, since this is the period when the majority of the germ cells free in the body cavity throw off the polar body and mature. Altho Tennent has found three bodies similar to those designated by authors as "polar bodies," no authentic proof is recorded of more than one polar extrusion in the maturing germ cell of a redia or sporocyst.

In summary, it may be said that the study of the germ cells in the rediae of *Cercaria flabelliformis* supports the thesis that true parthenogenesis takes place here; that the germ cells are traceable to a mesodermal cell mass in the region of the blind end of the gut; that a single polar body is extruded; and that maturation takes place without reduction.

It is not surprising that the details of the germ layers have not been worked out in the fertilized trematode egg, because of the yolk inclusions which obscure developmental stages and no doubt modify the behavior of the segmenting cells. Yet it is regrettable that no attempt at the precise origin of the germinal layers has been made on germ balls within the sporocyst or redia. Without any effort at this exact study of the problem the writer has followed in the living rediae of *Cercaria pellucida* and *C. konadensis*, and in the sporocysts of *C. dendritica* the development of the germ balls from the single mature ova, thru unequal divisions into two, three and five cells, up to the morula stage.

PARTHENITAE (SPOROCYST AND REDIA)

Since the classic work of Thomas (1883) on the life-history of *Fasciola hepatica*, it has been the common custom to define the sporocyst and redia in terms of stages in the life-history of the trematode. The sporocyst is the metamorphosed miracidium, and the redia arises within the sporocyst. The cercaria is the parthenogenetic offspring of the redia and develops into the adult trematode. While this represents a so-called typical life-history, it is

worth while to inquire into the facts and see if the outlined sequence of events is always followed. In some cases the sporocyst is the mother of the cercaria, in which case the redia cycle has been omitted. The accompanying table (III) shows that of the fifteen species treated in this paper eight have cercariae derived directly from the germ cells of the sporocyst. Of the seven remaining, five are known to come from rediae, while the parthenitae of the other two species of larvæ are not known.

TABLE III
GERMINAL EPITHELIUM

	PARTHENITA		NON-LOCALIZED	LOCALIZED
	SPOROCYST	REDIA		
Monostomata				
1 *Cercaria pellucida*		x		x
2 *Cercaria konadensis*		x		rachis
Holostomata				
3. *Cercaria flabelliformis*		x		x
4 *Cercaria ptychocheilus*		?		?
5 *Tetracotyle piprentis*		?		?
Distomata				
Xiphidiocercariae				
6 *Cercaria crenata*	x			x
7 *Cercaria glandulosa*	x			x
8 *Cercaria diaphana*	x		x	
9 *Cercaria dendritica*	x			x
10 *Cercaria micropharynx*	x		x	
11 *Cercaria racemosa*	x			x
Echinostome cercariae				
12 *Cercaria trisolenata*		x		x
13 *Cercaria biflexa*		x		x
Furcocercariae				
14 *Cercaria gracillima*	x			x
15. *Cercaria tuberistoma*	x			x

Types of development are characteristic of certain groups. The Monostomata, Holostomata, and Amphistomata and usually the echinostome cercariae develop within rediae. The xiphidiocercariae and the furcocercariae arise from sporocyst tissue. A considerable modification of a typical life-history, such as is found in *Fasciola hepatica*, is displayed among various groups of Digenea. In 1835 von Siebold described a viviparous monostome larva under the name of *Monostomum mutabile*, in which the miracidium bursts the egg-shell while it is still within the uterus. Within this miracidium, without any metamorphosis into a sporocyst, there develops a single redia. *Schistosoma japonicum* has two sporocyst stages, of which the former is covered with a smooth and the latter with a spinous integument (Leiper and Atkinson, 1915:202). This worm has no redia stage, for the cercariae develop within the secondary sporocyst. Cercariae and rediae develop side by side in the rediae of *Cercaria flabelliformis*.

The sporocyst is much simpler than the redia. It is merely a sac with ectoderm covering, and at times a secretory integument. Occasionally one end is partially muscular. From the inner wall of this sac arise the germ balls

that grow into the parthenogenetic individuals. In the simplest types the germinal cell mass consists of the entire internal layer lying next to the ectoderm. Such a type is seen in *Cercaria diaphana* (Fig. 79), and in *C. microphrynx* (Fig. 94). In the majority of cases, however, the germinal tissue is localized at one end of the sporocyst. In two cases at least there is the differentiation of a muscular attachment organ at the antipodal end (*C. dendritica*, Fig. 87; *C. racemosa*, Fig. 105). In the furcocercariae, *C. gracillima* and *C. tuberistoma* (Figs. 147, 157), there is a rhizoid-like attachment at the germinal end. In these cases there seems to be some evidence for regarding the germinal layer as localized at the end opposite the potential mouth.

The redia is the type of the life cycle normally developing within the sporocyst. Its organization is much more complex than that of the sporocyst. There is a well-developed oral aperture, a muscular pharynx, and a sac-like gut. There is a birth-pore just behind the collar region, on the left side, slightly ventral. Two projections, usually in the posterior part of the body, readily differentiate the redia externally from the shapeless sporocyst. With some justification Ssinitzin (1911:76) regards these projections as comparable to an originally bifid tail of the cercaria as in Bucephalus. In the cephalic region around the pharynx there is a nerve complex of highly differentiated nerve cells and nerve fibers. These are distinguishable as a central nerve ring, with four anterior and four posterior trunks. The posterior trunks do not develop far caudad. The integument is well developed and thick, and muscular layers within it play an important rôle in the movement of the redia, whereas the sporocyst depends almost entirely for its movement on the motility of the larvae within it. In the mature redia the germ tissue is always localized at the posterior extremity of the body.

The development of the germinal tissue of sporocyst and redia has been shown to be the result of the maturation of parthenogenetic eggs. The significant correspondence between the localized germinal epithelium of the parthenita and that of the cercaria may be pointed out here. In most cercariae the male germ cells are aggregated into a definite number of testicular masses, in most cases, two. In the apharyngeal furcocercariae (the probable larvae of the Schistosomatidae) the number of germ masses is larger. The data compiled in Table IV, on the better known Schistosomatidae, show that the number of the testicular follicles varies from four to five in *Schistosoma haematobium*, the mammalian parasite (Looss, 1899:658) to about 134 in *Bilharziella polonica*, the avian parasite. The origin of these testes is not described in any case. In all of the adults the sexes are separate. In *Cercaria gracillima* (Fig. 149) the testicular masses are proliferated from a germinal mass at the posterior extremity of the body, ventral to the excretory bladder. They are numerous; some twenty-four or twenty-five masses are found in this region at this stage of maturity. Moreover, the female cell masses are also present in the species at this larval stage, showing that the animal is not primitively unisexual, but hermaphroditic. It would be only one step further back in the phylogeny of the group to assume that the hermaphroditic cell masses and

TABLE IV

MALE GERM CELLS OF THE BETTER KNOWN SCHISTOSOMATIDAE

SPECIES	*Gigantobilharzia acotylea* Odhner 1910	*Ornithabilharzia kowalewski* (Parona and Ariola) 1896	*Bilharziella polonica* (Kowalewski) 1895	*Bilharziella pulverulentula* (Braun) 1901	*Austrobilharzia terrigalensis* S. J. Johnston 1916	*Schistosoma bomfordi* (Montgomery) 1906
NO. OF TESTICULAR FOLLICLES	many	many	134	110	18–20	61
LOCATION OF TESTES	esophagus to posterior end	chain in posterior quarter of body	entire region behind genital atrium	lateral to zig-zag unpaired gut	second quarter of body	three-sevenths entire body length
HOST	*Larus fuscus*	*Larus melanocephalus*	*Anas boschas* *Anas crecca* *Fuligula cristata*	*Anas querquedula*	*Larus novae-hollandiae*	*Bos indicus*
LITERATURE CITATION	Odhner 1910:383	Parona and Ariola 1896	Kowalewski 1896 Parona and Ariola 1896 Odhner 1912	Braun 1901a:947 Odhner 1912	Johnston 1916: 234	Montgomery 1906a:7
HABITAT	West coast Sweden	Mediterranean Sea	Lemberg, also East coast of Gotland	Dongola, Sudan	Terrigal N. S. Wales	India

MALE GERM CELLS OF THE BETTER KNOWN SCHISTOSOMATIDAE—*Continued*

SPECIES	*Schistosoma indicum* (Montgomery) 1906	*Schistosoma bovis* (Sonsino) 1876	*Schistosoma spindalis* (Montgomery) 1906	*Schistosoma mansoni* (Sambon) 1907	*Schistosoma japonicum* (Katsurada) 1904	*Schistosoma haematobium* (Bilharz) 1852
NO. OF TESTICULAR FOLLICLES	5–9	6–8	6–7	8	6–8	4–5
LOCATION OF TESTES	alternate, zig-zag behind ventral sucker	?	?	limited area	limited area behind acetabulum	anterior one-fourth of body
HOST	*Equus caballus* *Equus asinus* *Bos indicus*	*Bos* spp. *Ovis* spp.	*Bos indicus*	man	man, cat, dog	man *Ceropithecus juliginosus*
LITERATURE CITATION	Montgomery 1906:20	Sonsino 1876 Montgomery 1906a:14	Montgomery 1906a:10	Leiper 1916:411	Katsurada 1914:367	Looss 1895:181 Leiper 1916:411
HABITAT	India	In cattle, thruout Orient, in sheep, Sicily	India, Sumatra	Africa, Central America, South America, Antilles,	Japan, China,	Africa, Western Asia

the germinal epithelium of the parthenitae arose from a common type of germ cell. In other words, the germ cells of cercariae and parthenitae are homologous. Stages in the phylogenetic development of the germinal epithelium may be outlined thus:

1. Germinal epithelium non-localized. Example, *Cercaria diaphana* (Fig. 79), *C. micropharynx* (Fig. 94). Sporocyst cycle.
2. Germinal epithelium localized; no mouth or suctorial apparatus. Example, *C. glandulosa* (Fig. 67). Sporocyst cycle.
3. Germinal epithelium localized; suctorial disc or attachment organ opposite germinal cell mass. Example, *C. dendritica* (Fig. 87), *C. racemosa* (Fig. 105). Sporcyst cycle.
4. Germinal epithelium localized opposite a true oral aperture, with pharynx and gut present. Example, *C. flabelliformis* (Fig. 43). Redia cycle.
5. Germinal epithelium localized and specialized into two sorts of conjugating germ cells, male and female isogametes. (Theoretical.)
6. Male germ cells proliferated in numbers from the mass of germinal tissue at the posterior end of the body; female germ cells more highly differentiated. Example, *C. gracillima* (Fig. 149). Cercaria stage of hermaphroditic cycle.
7. Germinal cells massed into a small number of specialized glands, called testes and ovaries. Example, *C. pellucida* (Fig. 18). Cercaria stage of hermaphroditic cycle.

CERCARIA (GENERAL)

The cercaria is the offspring of the parthenita. It is a highly specialized individual, homologous to the immature redia or the sporocyst. Its specialization has been accounted for by Ssinitzin (1910:38-56) because of 1) a considerable period of free-swimming life, during which it acquired a tail, and 2) a change to parasitism in the vertebrate, which was at first facultative, but later became obligatory. There are two types of modified characters to be accounted for in the cercaria, in addition to the original characters common to parthenita and cercaria. The tail, the well-developed muscle complex, the nerves innervating the muscle system, together with the salivary glands and the sensory papillae—all of these bear evidence of a long period of independent life. When the organism became parasitic, first ectoparasitic, later endoparasitic, the highly developed muscular suckers with their nerve tracts were further developed, while the stylet organs and cystogenous glands were differentiated. The muscular specialization was of primary importance within the host, while the cyst served to protect the worm during the period of transfer from larval to definitive host.

The cercaria varies in size, altho it is fairly constant for a particular family or genus. Holostome larvae reach a size of 0.63 mm. in length and 0.35 mm. in width (*C. ptychocheilus*). On the other hand some of the xiphidiocercariae are much more minute, 0.18 mm. in length by 0.09 mm. in width (*C. micropharynx*).

There are two types of movement in the cercaria aside from the apparent contraction and expansion of the body. One of these is concerned with the forward movement of the animal and depends on the coöperative action of the suctorial organs and the general bodily musculature. The other is caused by the flagellate action of the tail. The movement of the cercaria along a forward path reminds one of the rythmic action of a measuring worm. The oral sucker is always used as one organ of attachment, and the ventral or caudal suctorial disc supplies the other anchorage. With these two organs of attachment, the larval worm applies the oral disc to the object of contact, while it draws the posterior portion of the body forward by the contraction of all the longitudinal muscles. This places the posterior attachment advantageously near the oral disc, so that a relaxing of the longitudinal muscles and a synchronous contraction of the transverse muscles throws the cephalic portion of the worm far forward. In the forms with well developed musculature, such as monostome and echinostome species, the larva may appear discoid on contraction, while the expanded worm will assume a length several times that of the normal body.

All groups of cercariae possess an oral suctorial organ. For the second attachment organ there is a variety of accommodation. Undoubtedly the most advantageously formed organ of this second type is the one found in the Amphistomata, where there is a powerful suctorial disc at the posterior end of the body.

Among the distomes there are many types of posterior suctorial organ, ranging from those with a prominent acetabulum not far from the caudal extremity, as in *Stomylotrema pictum* (Crep.) (Looss 1899:629), to those with a poorly developed acetabulum more cephalic in position. In the latter case there are frequently found auxiliary locomotor organs, such as those in the posterior pockets of the xiphidiocercariae. In some species there is only a suggestion of a paired suctorial organ, as in the larvae, *Cercaria crenata* (Fig. 55), and *C. diaphana* (Fig. 76). In others there is the additional spinose complement (*C. glandulosa, C. dendritica, and C. micropharynx*). These spines are of important function on rough surfaces where the disc can take hold with difficulty. Altho there is considerable difference in the rapidity of movement of the various species studied, *C. glandulosa* was by far the most rapid in movement of all the cercariae observed. The spinous outgrowth of the acetabulum is of advantage in locomotion, catching hold where the unarmed sucker can not operate (*C. glandulosa*, Fig. 60; and *C. gracillima*, Fig. 142).

Muscular development in the holostome larva is confined entirely to the suctorial apparatus, since there is no distinct tail portion. This type of sucker is derived from the distome type. With the translocation of the genital opening to the posterior end of the body, the primitive genital pore has come to be used as an accessory suctorial organ (*Cercaria ptychocheilus*, Fig. 47). The most unique modification is found in the tetracotyle type. Here there have arisen two lateral accessory suctorial grooves (Fig. 41), and lappet modifications of

the acetabulum. All of these come to be enclosed in a common pocket which acts as a large sucking cup (Fig. 40). There is practically no locomotion in these species, since movement is confined almost exclusively to the sucking reflex.

In the monostome no acetabulum is present, yet the cercaria performs the processes of locomotion *par excellence*. The pair of posterior locomotor organs replaces the acetabulum in the measuring worm movement. In *Cercaria pellucida* and *C. konadensis*, as well as in *C. urbanensis* Cort, these organs consist of posterior inpocketings of the integument. In *C. imbricata*, Looss (1896, Fig. 151) there is an internal pocket. In *C. ephemera* Nitzsch (Ssinitzin, 1905, Fig. 75, 76) there are hook-shaped spines. Cort (1915:15) finds that they "apparently have no suctorial function, since no muscles are present and the central cavity contracts while the projection is extended." A careful study of living and preserved specimens of *C. pellucida*, *C. konadensis*, and *C. urbanensis* shows that these three American species have no spinose or other integumentary modifications. However, their function is found to be distinctly suctorial, and not "analogous to setae," as Cort believes. Typical drawings for the locomotor organs of any of these three species are shown (Figs. 16, 17). As will be seen in figure 16, there are four muscles which are attached to the pockets. By a contraction of the pair *xx* the pocket disc is applied to the surface of the contact body; by a relaxation of *xx* and a contraction of *yy* the pocket is released and pulled forward by the general bodily contraction. This has been observed repeatedly in so convincing a manner that it leaves no doubt as to the structure or function of the organ. In addition, in *C. konadensis* (Fig. 21) a group of glands just anterior to the locomotor pockets pour out a mucous secretion at the time when the disc is applied to the contact organ. The locomotor pockets perform a similar function and in a similar manner to that of the secondary suctorial disc or acetabulum of amphistome or distome, altho these organs are in no sense homologous.

The significance of the spines in connection with the caudal locomotor pockets of distomes has been regarded by Leuckart (1886:128) as deserving special consideration. In *Cercaria armata* he considers them as serviceable in keeping the tail attached to the body after the constriction between the two parts has become deep. Looking into the phylogenetic significance of the spines of the same cercaria species, Ssinitzin (1911:68) regards them as indicating a bifid ancestral appendage of a caudal nature. In view of the fact that these pockets actually function similarly to the locomotor pockets of the monostomes, and are more than likely the ancestors of the monostome type of pocket (Fig. 12), it seems hardly worth while to find a more obscure meaning in the structures.

The tail is the portion of the cercaria showing preëminently the adaptation of the organism to free-swimming life. In such forms as *C. setifera* (Monticelli, 1914), *C. pennata* and *C. plumosa* (Ssinitzin, 1911, Figs. 76-79), the prolonged free-swimming existence has given rise to setae, spines and scutes.

The tail arises as a median posterior protuberance, bilaterally symmetrical, and is, according to the views of Ssinitzin, phylogenetically a paired organ. This thesis is supported, in part at least, by the fact that the excretory trunks arise as paired organs in both the body and the tail. In the furcocercariae the caudal tubules remain separate in the rami of the tail and also in the "eyelet anastomosis" at the junction of the body and the tail. There develops in the tail the usual complement of muscles, a transverse layer externally and a longitudinal group more median. Within the cylinder of muscles is the group of parenchyma cells surrounding the excretory tubule.

In the tails of distome cercariae (Figs. 99, 133) the excretory vessel is a paired structure, separated in the middle by a parenchymatous partition with one or two nuclei in each section of 7 μ thickness. Some schistosomatid larvae have, in addition, eleven or twelve pairs of oblong cells just lateral to the excretory vessel. The tail of the monostome is characterized by extra large longitudinal muscles with prominent nuclei. The portion within the longitudinal muscle cylinder differs in structure in individual species. In *C. pellucida* there is one ring of very large parenchyma cells situated around the excretory vessel. There are eight to ten cells to each transverse plane of 7μ. In *C. konadensis* and *C. urbanensis* there are glandular cells within the parenchyma ring; they are large and crowded with granules. In both of these species (Figs. 25, 32) these cells are arranged in six paired groups. In *C. konadensis* there are many cells to each member of the group, arranged in pyramidal fashion with the apex directed distally. Thus the largest cells in each group (Fig. 27) are proximal. These cells lie next to the excretory vessel. Cort has described the cells of *C. urbanensis* thus: "extending the length of the tail and forming a core are two rows of long cells which are close together and have their long axes parallel with the length of the tail. . . . They are full of heavy staining granules. . . There is nothing suggestive of the possible function of these cells." He has failed to observe the exact number of these cells (six pairs) and is in error in considering them as a core extending the whole length of the tail, for they alternate with non-glandular tissue in about half of the extent of the organ. Their structure is probably glandular. In *C. urbanensis* these cells arise from undifferentiated parenchyma cells (Fig. 33). They soon appear as falciform cells in trans-section (Fig. 34), separated in a median sagittal plane by a partition arising between two intermediate parenchyma cells, which soon differentiate into a muscular lamina. The lamina arises before the excretory tubules differentiate as distinct lumina among the parenchyma cells. Thus the bilateral symmetry along the median sagittal plane is well shown. The excretory vessel is single in the mature *C. pellucida* and *C. konadensis*, but remains paired in *C. urbanensis*.

Looss (1893:24-28) cites the epithelial cells of the tail of cercariae as good examples of "Blasenzellen," where all cell elements of the mesenchyme usually become "Blasenzellen", and where no true glands take their place. The study of *C. konadensis*, *C. urbanensis*, and *C. gracillima*, shows that axial cell glands are present, and that they are derived from the parenchyma. Moreover

where these special gland cells are not present, as in *C. pellucida*, the parenchyma cells are more vesicular than where they are present. The writer is in accord with Looss's view that there are no indifferent cells remaining in the tail. Hence the tail, when separated from the body, can not metamorphose into a sporocyst or redia, as the older writers believed (Pagenstecher, 1857:15).

INTEGUMENT

The covering of trematodes and cestodes has been the subject of considerable controversy. Four main theories have been proposed. The Blochmann theory (1896) assumes that the cuticula of trematodes and cestodes is a true morphological cuticula secreted by the hypodermis, as in other invertebrates. A second theory, presented by Brandes (1892), postulates that trematodes have no subcuticula in the true sense of the term, and what has been considered as such is nothing more than the true parenchymatous connective tissue. Nevertheless, the body covering is a true cuticula, secreted by special glandular cells of epidermal origin just beneath the cuticula. The presence of apparent nuclei in the cuticula has revived the old idea of Wagener that the cuticula is a metamorphosed epithelium. Goto has subscribed to this theory in his study of ectoparasitic trematodes (1894:6-13), defining three layers, an outer cuticula, a subcuticula, and a basement membrane. This is also the interpretation Monticelli has put on the body investment of *Cotylogaster michaelis* (1892:189), which he claims to possess an "ectoderma sinciziale di aspetto cuticuloide." More recently Cary (1909:646) has advocated this view. Pratt (1909:721) is inclined toward Leuckart's theory that the cuticula is of parenchymatous origin, a derivative of the peripheral portion of the parenchyma.

The species of larval trematodes studied by the writer are uniform in showing that the epidermal layer, developing into a syncytium in many cases, is present in the early stages of the sporocyst, redia, and cercaria. In the parthenitae, especially in the redia, this layer may persist until the germ balls within are ripe and ready to escape. In the cercaria the epidermal tissue is present in early life as a syncytial layer investing the larva. In the mature cercaria it is sloughed off. The "cuticula," when present, arises from below the epidermis. It is a discrete layer underneath the epidermis, or it impregnates the epidermis from below. In the latter case the nuclei are always superficial, usually rising above the surface as small tuberosities.

In the monostome group, the redia possesses a syncytium of ectodermal cells impregnated here and there with granules of a secretory nature. The cercaria develops a well-defined epidermis which later (Fig. 37) becomes syncytial and is sloughed off. Underneath this the "cuticula" is distinctly cut off from the epidermis on the outside and from the mesodermal tissue beneath. Among the latter are the special parenchyma cells with aciculate pseudopodia, corresponding to Blochmann's "Epithelzellen" (1896:7). These differentiated parenchyma cells have no connection with the "cuticula" in

the developing or mature cercaria of this group. A non-nucleated epidermis is shown in the process of sloughing off for the hemistome cercaria (*C. ptychocheilus*, Fig. 54). Underneath is a distinct layer of "cuticula." Beneath the "cuticula" is a lining of transverse and longitudinal muscle fibers. Median to the complexes of the longitudinal muscles are the complexes of the connective tissue. The whole structure, from the inner wall of the "cuticula" thru to the free parenchyma, is infiltrated and bound together into a single mass by a mucoid secretion. This secretion is indifferent to stains. The epithelial cells of the complex send out long processes toward the integument, so that the processes penetrate into the latter. These cells suggest gland cells, concerned with the secretion of the "cuticula." They are not potentially different from the underlying parenchyma.

Among the distome larvae the writer has studied the "cuticula" problem for echinostomes, schistosomes, and xiphidiocercariae. The redia of *C. trisolenata* possesses an ectodermal reticulum in which are found large vesicular nuclei. This covering is impregnated with large granules which are indifferent to stains. In the cercaria of this form (Figs. 128-133), there is an ectodermal layer present, very thin, with the nuclei arising from the surface as minute tuberosities. Beneath this is the thick layer of "cuticula." The epidermis has been lost in the tail. No "Epithelzellen" are visible in the mesenchyme complex. For the schistosome larva, *C. gracillima*, there are definite nuclei present as minute papillations rising above the surface of the epidermal layer. The sporocyst of this form has no "cuticula." The body wall consists of a single layer of ectoderm cells, arranged end to end, the nuclei of which are oval to subspherical. In the distome, *C. glandulosa*, the sporocyst wall is composed of a single layer of epidermal cells, with falciform nuclei. In the cercaria the epidermis is present only in individuals where the tail is still attached. Here nuclei are present in the peripheral layer of the body, but are not found in the covering of the tail. The "cuticula" is a thin envelope around the circular layer of muscles.

The study of these trematodes with reference to the problem of the integument has led the writer to set aside the view that the "cuticula" is ectodermal in origin, because the ectoderm is superficial, lying outside the "cuticula." The impregnation of this layer with cuticular granules might lead one to believe that the two layers are one, but the earlier history of the layers shows that this conception is erroneous. No hypodermis is found in any of the species studied. Consequently the Blochmann theory can not hold for these species. No special gland cells have been found to support in its entirety the theory of Brandes. On the other hand the evidence of this study points to the sustaining of Leuckart's theory of the parenchymatous origin of the basement membrane on the following grounds. 1) In all the species the basement membrane arises from tissue beneath the ectodermal layer. 2) In all cases where there is an ectodermal layer only (in sporocysts), no basement membrane is found. 3) The heaviest layer is found in species where the parenchyma has a widely diversified potency, such as salivary, cystogenous, locomotor and

mucin glands. 4) The "Epithelzellen" of the monostomes and holostomes (Figs. 37, 54) are characterized by large vesicular nuclei and vacuolated cytoplasm, similar to the "Blasenzellen" of Schwarze (1886) and Looss (1893). They are modified parenchyma cells differing from the underlying layers not in potency but in location. 5) As the secretory cells for the basement membrane, these parenchyma cells have developed long acicular pseudopodia toward the membrane and, in the larval holostomes, have penetrated into it. All of these data point toward the parenchymatous origin of the basement membrane.

PARENCHYMA

Soon after the fundaments of the digestive and nervous systems of the cercaria are laid down, certain cells of mesodermal origin of the germ ball become ovoid and are filled with milky white granules. These are cystogenous cells, the "Stäbenkörnchen" of the German writers and the "cellules à bâtonnets" of the French. They develop most commonly in monostomes, amphistomes, and such distomes as form a heavy cyst.

Other portions of the mesoderm are differentiated as the germinal epithelium and the muscle layers. The remainder of the mesodermal cells is for a considerable time potentially great, and remains undifferentiated (Looss, 1893:29). They constitute the parenchyma. Looss has compared these cells of the mesoderm to the cambium of the plant. They are the "nichtveränderten Zellen," on the multiplication of which depends the growth of the minute larva to the relatively large adult. As the animal grows the cells of this region become more vesicular, vacuoles appear within the cytoplasm, and acidophilous granules appear within the cell. The intercellular spaces become more and more prominent. The cells are held together by bands of ragged connective tissue which, for the most part, is the outgrowth of the interstitial cells. Within this parenchyma complex there appear large tubular lumina in certain definite regions, and, leading into these, tubes and smaller tubules. These are the excretory tubes; at the ultimate ends of these are found the capillaries and the flame cells (Looss, 1892:162; Thomas, 1883:116-118). In the schistosome cercariae studied the main group of cilia is not at the extreme ends of the ducts, but in a pocket in the posterolateral part of the main trunks (Figs. 143, 145). It is of importance to emphasize here that these excretory trunks and tubes are not lined by a wall of specialized cells, but are merely lumina among certain cells of the parenchyma. It seems highly probable that Looss's view is correct as regards the flame or "Trichter," that it, too, is an intercellular lumen, into which the parenchyma-cell cilia protrude, and that it is not in a hollowed-out cell. The cilia are definitely outgrowths of the single cell at the head of the capillary (Fig. 138), a cell which is differentiated from the sister cells of the parenchyma by the possession of a much smaller nucleus and densely granular protoplasm.

MUSCULATURE

The muscle systems of the parthenitae and the cercariae are confined, for the most part, to the peripheral and splanchnic regions. The peripheral muscles consist of an outer series of radial muscle fibers and an inner series of longitudinal fibers. A third series, the dorsoventral, which is common in the adult forms, is suggested at times in the body of the cercaria. The muscles of the intestinal tract consist of a longitudinal and a circular series.

The peripheral system lies directly beneath the basement membrane. It opens interstitially to permit the growth of the processes of the parenchyma cells which secrete the basement membrane. The outermost layer is the circular series. It may consist of a single band one cell in thickness or it may include a cylindrical band several layers thick (Figs. 37, 54, 97, 128). Within this is the longitudinal series. Usually here the individual fibers of the bundles are separated from one another by a considerable interval. The fibers are longer and fewer than those of the circular series. A section of an adult trematode shows, in addition to these, an oblique series of fibers. These oblique fibers give the appearance in section of a diamond pattern. In another type, the dorsoventral, the fibers run at right angles to the frontal plane. In the holostome cercaria (Fig. 54) no such series is found, altho the longitudinal series is so arranged that the fibers are on edge and might be taken for the dorsoventral series. The view of Bettendorf (1897:315, 316) that the "Epithelzellen" of Blochmann are really longitudinal muscles, can not be considered valid, since in the same sections the former are indifferent to stains and the latter are deeply stained by the same methods of technic.

In the oral and acetabular suckers and frequently in the pharynx there exist the transverse, longitudinal and oblique series of muscle fibers, interwoven into an inseparable complex. These are best developed in the Amphistomata. Since the redia which produces germ balls is an adult and the cercaria is an immature individual, it is not surprising that the pharynx of the redia is fibrous, with few nuclei and large vacuoles, while the pharynx and suckers of the cercaria are composed of cells practically undifferentiated. In the rediae the fibers can be traced to the myoblasts.

The main deep-seated system of muscles for the cercaria consists of the muscle band series of the digestive tract. In the holostome (Fig. 54) an additional muscular activity has been assumed by the cirrus pouch. Aside from these no muscle striae are developed in connection with the genitalia in the larva. The ceca of the digestive tract are covered with an outer and an inner series. The former are longitudinal fibers and the latter are circular fibers. This is in conformity with the muscular layer studies made on other Platyhelminthes.

Histology of the muscle cells. When Bettendorf (1897) showed the connection between the muscle fibers and the myoblasts an important step was made in the knowledge of the intimate structure of the trematode muscle cell. The present study corroborates Bettendorf's work. The nuclei of

the myoblasts are oval (Figs. 118, 119). The cells very early send out long protoplasmic strands along well defined paths. While the processes from the myoblasts may emerge from any part of the cell, the longitudinal strands are always directed in a longitudinal plane, and the circular fibers are always circular. A unique picture is presented at the point where the furcae of the digestive tract arise (Fig. 118). Here there are two anterior processes running cephalad, and three strands proceeding caudad along each cecum. The chromatin in the nucleus of the myoblast is usually confined to the karyosome.

ARMATURE OF THE TREMATODE

The miracidium and sporocysts are not ordinarily provided with hooks or any piercing armature. The redia is usually conspicuous because of its oral sucker, pharynx and gut, and not because of any armature. In the cercaria, however, are found, even in some of the most delicate species, spines covering the basement membrane, especially in the region of the head. In the special group of the stylet cercariae the stylet is the larval organ which is of specific systematic value.

It is not a universal rule, however, that all rediae and sporocysts are unarmed. At times a modification of the posterior wall of the redia is produced as in the redia of *C. biflexa*, where the terminal organ is spinose (Fig. 141). Leiper and Atkinson (1915:202) found the second sporocyst generation of *Schistosoma japonicum* to be covered with a spinous integument. More conspicuous is the prepharynx organ of the redia of *Cercaria pellucida* (Fig. 7). This organ is four-lobed, and has on the outer side of each lobe long spines projecting forward and small spines directed laterad. The use of such a weapon within the soft parts of the host tissue produces untold injury.

No armature has been observed on the body of any monostome cercaria. The holostome, *Tetracotyle pipientis* (Fig. 47), has a spinose covering over the entire body and special spines in the region of the acetabulum and accessory suctorial grooves. Spinose modifications are common in the distome group, and in some cercariae, setiferous modifications of the tail. The types which the writer has examined have the armature confined to the body. They will be discussed under the headings of 1) general body spines, 2) spines of the oral aperture, 3) collar spines of the echinostomes, and 4) the stylet organ of the xiphidiocercariae. In addition there are the spines at the posterior end of the trunk in the caudal pockets. Their probable locomotor function has made it necessary to consider them in another place.

In many cercariae there is a tendency for the entire bodily integument to become modified so that the surface bristles with needle-like spines. These are usually arranged in a regular diamond pattern, and are more fully developed at the anterior end of the body than in the caudal portion (Figure 90). This condition is found in some xiphidiocercariae and some echinostomes. The spines are always pointed forward. They are more fully developed in the anterior region of the body.

Of a somewhat more limited distribution is the oral armature of spines in the schistosomatid *C. gracillima* (Fig. 142). These spines are turned into the body with the inpocketing of the oral sucker-pouch, so that the animal in the condition of contraction appears perfectly aspinose except for the armature of the acetabulum. But with its protrusion the oral sucker is crowned with a solid cap of spines.

The hood of spines of the echinostome group is specialized and valuable in systematic work. It is usually an incomplete ring, consisting of a circlet of spines around the dorsal side, extending ventrad into the middle half of the body. Dietz (1910) has sketched 63 figures of spine characters and numbers in his monograph on the Echinostomidae of birds. The adult echinostomes of North America have received little attention and in consequence of the difficulty in working out the exact spine number in the larva a description of the specific spine characters of the cercariae will not be worth while until more attention is given to the adults of the family.

The stylet is the unique larval organ in the group of the xiphidiocercariae. It might be more properly called a quill than a stylet, for its value as an organ of piercing is questionable on account of its frailty and frequently disadvantageous leverage. It is a mucoid structure, situated in the dorsal wall of the oral pocket, well supplied with muscles to work it in any direction anteriad and laterad. It is fully formed only in the mature cercaria, and is carried into the cyst (Figs. 84, 85). Quite generally the stylet is recognized as of specific systematic value, and is therefore figured in systematic descriptions (Lühe, 1909:189-200), but the stylets as they are figured are so generalized as to be of little value in the identification of species. The stylet is of specific value, but this value lies in the details of the organ rather than in the general outline. (See Figs. 57, 61, 77, 83, 91, 102).

The stylet is usually a weak organ mechanically and poorly levered. However, it is resistent to chemicals and indifferent to dyes. The stylet of *Cercaria glandulosa* is extremely delicate, so that it goes to pieces immediately when a cover glass is pressed down on a water-mount of the worm. The stylet, as a rule, is hard to observe in preserved mounts.

GLANDS OF THE LARVAL TREMATODE

Glandular organs in the trematode may be distinguished as dermal, salivary, mucin, cystogenous, genital, and locomotor. The dermal glands are those imbedded in the subdermal tissues, are unicellular, usually flask-shaped, and have a small duct opening to the exterior. The salivary glands include all of the unicellular glands which open into the digestive tube. Mucin glands are paired, right and left groups of one to several gland cells emptying into the oral pocket thru long attenuate ducts. Since mucin is a constituent of salivary glands, these glands are modified salivary glands. Cystogenous glands are imbedded in the parenchyma and are usually filled with rhabditiform granules which superficially resemble the dermal rhabdites of the Turbellaria but are

not to be confused with them. The cystogenous glands function in the formation of the larval cyst at the time when the transfer to the secondary or definitive host is to be made. Genital glands, in the sense employed here, include only the auxiliary gland elements of the genital system and do not refer to the sex glands themselves. Locomotor glands arise in connection with the locomotor organs in the posterior part of the body.

The dermal glands are of adult significance. Looss (1894:125) has found them in all groups of adult trematodes studied, but he does not later (1896: 219, Fig. 176, *glcu*) record them for any cercariae except *C. vivax* Sons. No dermal glands have been found by the writer in the course of the present study.

Salivary glands are probably present in all groups of cercariae and in some rediae. In the simplest form they are nothing more than pyriform cells in the region of the digestive tube. Thus the monostome cercaria, *C. imbricata*, described by Looss (1896:195) as having a pharynx without a bulb, has unicellular glands massed around the tube in the pharynx region. The furcocercariae, with no true pharynx, have a similar group of cells in the pharynx region, so closely massed together as to lead Looss to considering them a true pharynx (1896:220, Fig. 176, *ph*). In structure these masses of glands in the furcocercariae look superficially like a pharynx (Fig. 142), but on cross-section the cells of the complex are found to be unmistakably glandular (Fig. 152).

A modification of the type of salivary gland just described has been observed in *Cercaria micropharynx*, *C. diaphana*, and *C. glandulosa*. In these species the cercariae show not only the muscular pharynx, but also a large group of gland cells around the digestive tract. In *C. micropharynx* (Fig. 93) the glands are prepharyngeal, grouped in a spherical mass around the oral chamber. They are minute cells, about 3μ in trans-section. The glands of *C. diaphana* (Fig. 76) exhibit a maximum glandular growth in the vicinity of the pharynx proper. Several hundred gland cells about 3μ in diameter surround the pharynx. A case of secretion along the entire digestive tract is found in *C. glandulosa* (Fig. 60). In this species the glands are much larger than in the two preceding species, about 6μ in cross section and 12μ to 25μ in length. They are formed along the entire course of the lumen, from the orifice to the blind end of the ceca, altho they are best developed in the region of the pharynx.

A distinctly different type of gland is that termed the "stylet gland." It is so-named because of its frequent occurrence coincidently with the stylet organ of the xiphidiocercariae. But since it occurs, too, in furcocercariae and in echinostome cercariae, where there is no trace of a stylet, the evidence supports the view that this type of gland is more generalized and more primitive than the stylet organ.

These glands are found in the cercariae of the distome groups examined by the writer, and in the redia of the holostome, *C. flabelliformis*. They are bilaterally symmetrical, lying outside the intestinal furcae, behind the region

of the pharynx. They open thru long-necked ducts into the oral pocket. The glands are in masses; they vary in the number of cells from four in each lateral mass of some furcocercariae (Fig. 144), to eight or ten in the stylet cercariae, while in the echinostomes they run as high as 110 on each side of the esophagus (Fig. 134). In general the cells are characterized by a densely staining granular protoplasm and a highly refractive nucleus, which remains hyaline when treated with hematoxylin dyes. Most interesting is the type presented in *Cercaria crenata* (Fig. 55), where there is a differentiation of inner and outer groups of the glands on each side of the gut. These groups have individual canals to their exit at the oral pocket. The outer series consists of six glands, comparatively small, 8μ to 9μ in diameter, goblet-shaped, extending caudad to the midacetabular region. They are finely granular and are best studied in living mounts. The inner series consists of five cells, two of which are situated just behind the pharynx and the other three postacetabular, thus causing the inner series to be divided into an anterior and a posterior group. These inner gland cells are 11μ to 15μ in diameter, and coarsely granular. Their difference in structure suggests a functional difference.

The mucin glands of the redia of *C. flabelliformis* are paired structures, lateral and dorsal to the digestive pouch, consisting of a single series of six cells which open thru a common tube into the pharynx region of the redia. The cells are similar in structure to the mucin cells of the cercariae of other groups, altho no such glands have been recorded from the cercariae of the holostome group. Only one other case has been reported for the redia, that for the parthenita of *Cercaria equitator* by Ssinitzin (1911:52, Fig. 50). In this redia the gland cells consist of a single cell with a wide duct to the pharynx region. A similar pair of unicellular salivary glands is figured by Looss for the miracidium of *Schistosoma haematobium* (1896, Fig. 113, *glcph*) and by Miyairi and Suzuki for the miracidium of *S. japonicum* (1914, Taf. 2, Figs. 1, 2). This occurrence of the mucin glands in the miracidium, redia, and cercaria of various groups, and the fact that they pass into the intermediate host along with the larva (La Rue, 1917), show that these organs are of fundamental importance in the economy of the worm.

That these glands are of more specific character than the ordinary salivary and epidermal cells of the trematodes is demonstrated by their differential staining reaction. The usual hematoxylin dyes show a great number of granular protein inclusions. Recently La Rue (1917) has shown that these glands in *Cercaria marcianae* have "mucus" in their ducts, because of the staining reaction with toluidin blue and thionin. However, since the glycoprotein of salivary digestion is mucin (Mathews, 1915:323), it is more exact to designate these structures as *mucin glands*.

A type of gland undoubtedly common to all cercariae is the cystogenous gland. It is a unicellular organ in the parenchyma just beneath the integument. In some groups this cell may be small and in the midst of parenchyma cells (*C. glandulosa*, Fig. 62). In other groups the cystogenous cell is very large and conspicuous as in the species *C. pellucida* (Fig. 14), *C. dendritica*

(Fig. 85), and *C. trisolenata* (Fig. 132). The material within the cyst cell is usually milky, semi-opaque, either homogeneous or granular. In most cases the contents consist mainly of the rhabditiform granules, which are indifferent to dyes. These granules are not attacked by weak acids or alkalies, but are digested by strong acids or bases. It seems probable that they are of a derived protein nature.

The formation of the cyst varies in the types studied. In the majority of the species the cyst is a firm envelope with a free space around the embryo, more or less filled with a watery fluid (Figs. 41, 84, 118). On the other hand, some of the cysts are more mucoid in structure, with a granular viscous inner portion and an outer jell (Fig. 11).

The method of encystment differs in different species. In the monostome where the encystment is rapid and an entire lot of mature cercariae encysts in two or three minutes after they are freed from the redia, the process is so rapid that the tail is not entirely cut off until the major portion of the cyst as formed (Figs. 9-11). Where the time of encystment is considerably longer, os in *C. trisolenata* and *C. dendritica*, the tail is discarded long before the process of encystment actually begins. Encystment is an adaptation on the part of the larva to the change in environment. In two cases studied it takes place within the liver of the primary host (*C. micropharynx* and *C. biflexa*). It is highly probable that in these forms encystment was the result of temperature stimuli, since the worms were secured in November when the winter had already set in. It is apparently an adaptation for "wintering over."

In only one group, the furcocercariae, has there been no record of encystment of the cercaria. Here the tail is dropped only under the pressure of the cover slip or when the worm begins to disintegrate. La Valette (1855:34) expresses this condition for his forms when he writes of the larvae: "Cercariae cystibus non indutae in animalium vertebratorum intestinis pereunt."

The phenomenon of encystment is one which has been observed by many investigators. It has been seen and described very accurately by La Valette, Moulinié (1856), Pagenstecher (1857), and a long line of later investigators. Moulinié refers to the studies of earlier workers on encystment, mentioning von Siebold (1835) and Steenstrup (1842). But the credit for the first record of encystment undoubtedly belongs to Nitzsch (1807). Later (1816) this writer records his observations on the encystment of *Cercaria ephemera*. The review of Nitzsch in Isis describes the process of decaudation and encystment as observed by Nitzsch, and shows that this worker expected the cyst to develop the following year. Fantham's criticism of Nitzsch is essentially unjust (1916:12), since Nitzsch considered the cyst to be dormant ands set dead.

The process of encystment has been described in detail by Thomas in his work on *Fasciola hepatica* (1883:129). Encystment here conforms to the rapid type described for the monostome *C. pellucida*. "The tail is sometimes shaken off before encystment begins, but, as a rule, the tail remains in connection with the body during the process, and continues to be energetically

lashed from side to side, until finally a more vigorous movement detaches it. The whole process is very rapid, and in a few minutes a layer of considerable thickness is formed, whilst its substance begins to harden."

EXCRETORY SYSTEM

The excretory system is the most delicate of the four important systems of the trematode. It can be worked out with precision in the living animal, but in preserved material it is impossible to find more than the main trunks of the system. In all of the cercariae and parthenitae described in this paper the excretory systems have been studied from living material. Altho there are many individual differences within groups, yet the fundamental uniformity of groups is evident.

A. The Monostomata. The main features of the excretory system of the Monostomata are the two main trunks arising from a common point just behind the median eye-spot or median pigment center, and proceeding posteriad and laterad to the posterior part of the body, where they join one another in the common vesicle. The bladder opens to the outside thru the excretory pore. which is not terminal but slightly dorsal.

The main excretory trunks are filled with large refractory granules, more extensively described on p. 42. The continuous circuit of the system provides for the transfer of granules and other waste products from right to left and reversely, dependent on the contraction and expansion of the several parts of the animal.

The bladders of the various species differ considerably in size and structure, but as a whole they may be placed in two sub-groups. In the trioculate forms, such as *Cercaria pellucida*, in dorsal view the bladder is distinctly trilateral when relaxed, with the excretory pore at the posterior horn. This same type is found in *C. ephemera* Nitzsch (Ssinitzin, 1905, Fig. 76), and in *C. imbricata* Looss (1896, Fig. 148), and also in *C. zostera* (Ssinitzin 1911, Pl. 1, Figs. 14, 15).

In action, however, due to the muscular movements of the posterior portion of the body, the anterior portion of the bladder may seem to be a separate organ opening into the bulbous posterior portion of the vesicle thru a constricted area. In the binoculate types, on the other hand, the bladder is spherical, with the excretory trunks emptying into the extreme lateral reaches of the vesicle. The excretory pore in these species is subterminal rather than terminal. The only binoculate species known are *C. lophocerca* (de Filippi, 1857, Pl. 1, Fig. 3), *C. urbanensis* (Cort, 1915, Fig. 5), and *C. konadensis*. Lebour (1907:443, Pl. X, Fig. B) describes the bladder of C. *lophocerca* as semilunar, but from her figure it appears more reniform than lunar. Cort does not describe the shape of the bladder of *C. urbanensis*, or state its size. The writer has found it to measure 50μ to 60μ in median sagittal line and 60μ in transverse section for preserved material. The excretory pore of this species is large, some 20μ in diameter; it is weakly muscular (Fig. 35). In *C. konadensis* (Fig. 29) the bladder is small, 14μ to 15μ in diameter. The excretory pore is correspondingly small, 3μ to 4μ in diameter, and weakly muscular.

The excretory system in the tail of monostomes is simple. It consists of a median tubule, with tributary laterals, which swell in the proximal region and empty into the common bladder of the trunk.

B. Holostomata. The excretory systems of Holostomidae and Hemistomidae are sufficiently different to require separate treatment.

1. Holostome type. No accurate or detailed description of the tetracotyle type of excretory system exists. De Filippi (1857, Fig. 26) has pictured two laterals for *C. vesiculosa*, arising from numerous tubules in the anterior part of the body. The connection of these tubes in the region of the bladder is not clear. Altho his sketch was made "to show particularly the lateral vessels," it gives no adequate conception of the fundamental vessels of the system. Brandes (1891:569) merely states that the "system reaches into all parts of the cone; an especially large canal passes longitudinally thru the anterior wall of the cone." Only a faint suggestion of the system is figured by Rosseter (1909, Fig. 17), for *Holostomum excisum* (von Linstow). Brown (1899, Fig. 11) has worked out an interesting but unusual type. In view of the lack of definite data concerning the excretory vessels of the holostomid group, it seems advisable to describe the system for the species *Cercaria flabelliformis*.

The excretory system of *Cercaria flabelliformis* is shown in figure 39. At the extreme posterior end of the worm, situated slightly dorsally, is the excretory pore. It is the opening of a relatively small bladder no larger than the pore itself. At its antero-lateral horns two large trunks arise, considerably inflated in their posterior portion. They may be traced forward along the inner reaches of the digestive ceca until they reach a place about two-fifths the distance from the anterior end of the larva. Here a transverse canal is found, with a median connection between the two trunks, and lateral transverse tubules. The lateral tubules drain the part of the larva posterior and lateral to them. Between them and the main longitudinal trunks are found a great number of anastomoses. Anterior to the median transverse canal the tubules spread out in fan-like arrangement, running to the sides and front of the worm.

Apparently this system was originally distome in character, but was made over to suit the needs of a modified distome larva. The longitudinals are clearly those of the Y-type so common to the excretory system of the distomes. On the other hand, the transverse tubes and the anastomoses of the postero-lateral reaches are new structures.

The entire system is filled with minute refractory granules which facilitate the tracing of the courses of the various vessels.

2. Hemistome type. This type has been worked out in faithful detail both in the larva (Diplostomulum) and in the adult. Hence a discussion of the excretory system of *C. ptychocheilus* will be limited to the points of divergence from the previously described species.

The earliest larvae of this group to be accurately figured are *Diplostomulum clavatum* (Nordmann) and *D. volvens* (Nordmann) (1832, Taf. II-IV). From the elongated bladder there arises a bicornuate structure which proceeds forward and outward for a short distance. A bifurcation of each cornu then

takes place, so that there are two pairs of vessels to proceed forward, an inner and an outer pair. They run forward to a plane in front of the middle of the body, where they unite and run cephalad as a single vessel. A transverse vessel is found posterior to this union; this vessel connects the two sides of the system. Brandes' diagram for the excretory system of *D. abbreviatum* (1891, Taf. 39, Fig. 17) differs from this type only in the details and not in the main features.

The system of *Cercaria ptychocheilus* (Fig. 49) has a long, attenuate non-muscular bladder dorsal to the posterior genital apparatus. It does not pair but gives off a single median longitudinal vessel, which proceeds forward to the midacetabular region, where it gives off the transverse vessel. The median longitudinal trunk then runs forward to the origin of the ceca. Here it gives rise to three antero-lateral vessels. These bend outward and backward, with numerous anastomoses, and finally unite with the lateral traces of the transverse vessel. The outer reaches of the transverse vessel give rise to many anastomoses which are conspicuous in the postero-lateral portion of the body.

The fundamental vessels of the holostome type are the paired laterals and the transverse vessel. Anastomoses and modifications have altered the system appreciably, but not beyond the ability to recognize in them a common type underlying the system, probably reducible to the Y-type of the distomes.

The entire system contains many medium sized refractory granules which oscillate back and forth thru the vessels at every movement of the animal. By unusual contraction of the worm, the granules are forced into the bladder and out thru the excretory pore.

C. Distomata. The distome cercaria has a simple type of excretory system, consisting of a posterior median bladder with two lateral longitudinal vessels in the body of the cercaria and a median longitudinal vessel in the tail.

1. The xiphidiocercariae. The excretory system of the stylet cercariae consists of a bladder, usually muscular, and a pair of lateral longitudinal vessels which arise from lateral cornua of the bladder. The primitive lateral system consists of three tubules, which emerge from the common lateral soon after the latter leaves the bladder. One of these tubules proceeds posteriad, while the other two run forward as inner and outer tubules. The single median tail vessel ends blindly near the posterior end of the tail; it sometimes receives tributaries, but this is not always the case.

The bladder is a median posterior structure opening to the exterior thru the dorsal pore. It is usually muscular, unpaired. It varies greatly as to size and shape. It may be pyriform (Fig. 90), obovate (Fig. 93), crenate (Figs. 55, 81), truncate or obtruncate (Figs. 60, 100), falciform (Looss, 1896, Fig. 146), or lunar (Looss, 1896, Fig. 179).

The physiological and morphological bladders are not always the same. The former may encroach on the lateral tubules in order to increase its capacity. This may consist of mere enlargements of the cornua without any change in structure (*C. glandulosa*, Fig. 60; *C. micropharynx*, Fig. 90). On the other

hand the needs for a muscular enlargement sometimes cause the muscularization of the cornua (*C. dendritica*, Fig. 81; *C. crenata*, Fig. 55; and *C. racemosa*, Fig. 100). In *C. diaphana* (Fig. 76) the modification of structure has taken place before the enlargement of the long median vessel and the lateral tubes.

The capillaries tributary to the lateral tubules are represented in their most simple form in *C. micropharynx*. The internal anterior vessel may move forward, as in *C. crenata*, or become rudimentary, as in *C. glandulosa*. The external anterior tubule is usually the most fully developed.

It is important to note that the lateral systems of the xiphidiocercariae never anastomose or coalesce in any way. Thus the median sagittal plane acts as a "watershed."

In the forms studied no large flame cells were found in the course of the excretory system. If any minute flame cells were present they were concealed by the thick integument.

The literature shows a paucity of observations on the flame cells of larval and adult distomes. Ssinitzin (1905) shows the details of the flame cells in *Gorgordera pagenstecheri* and in *Phyllodistomum folium*. They consist of an ameboid cytoplasm in which is imbedded a spheroid nucleus with rich chromatic inclusions. This cell is the terminus of the capillary (*cl*). It is ordinarily funnel-shaped, but when distended becomes deeply reniform. The junction of the flame cell and the capillary is marked by a considerable number of cilia which vibrate rythmically, giving rise to Ssinitzin's characterization, "vibratile tip cell of the excretory system."

A detailed study of the flame cell of the adult distome is given by Looss (1896:110; Figs. 72, 77) for *Distomum sanguineum* Sons. The details of the cell *per se* are not appreciably different from those given by Ssinitzin, but the distribution of the flame cells thru the body of the distome is described. There are four symmetrically paired groups of three cells each in the middle of the body, and one pair of two cells each in the anterior and posterior reaches of the body, making sixteen pairs of flame cells and capillaries in all (Fig. 77). This probably gives an indication of the arrangement of the flame cells in the typical distome. In *Distomum isoporum* (Looss, 1894, Fig. 103) six paired groups of ultimate tubules are figured with four flame cells to each group, making forty-eight flame cells in all. In *Distomum cylindraceum* (Fig. 163) there are six paired groups of capillaries with three flame cells to each group, totalling thirty-six flame cells. Thus the number of flame cells is not constant in different species but ordinarily remains constant for each species.

Looss (1894:249, 250; Fig. 186) suggests that the fundamental larval system is the fundamental system of the adult. Extension and modification occur thru a dichotomy of the existing capillaries and flame cells, and an encroachment of the tubules upon the capillaries. The greatest modification takes place during encystment, altho this is in no sense a metamorphosis.

Among adult American distomes the excretory system of *Microphallus opacus* Ward alone has been worked out with the exactitude of the European workers (Wright, 1912, Pl. 17, Figs. 1, 2). This form has the distome

Y-shaped bladder and cornua. There are only eight paired capillaries, and only sixteen flame cells. This condition constitutes a reduction of flame cells from the average types, a reduction which can not be entirely accounted for by the small size of the species.

2. The Echinostome type. This family of distomes is characterized by simplicity of detail in the excretory system except at the head of the main lateral vessel. The bladder is not markedly muscular. The pair of lateral vessels arise from the anterior median region of the bladder, and not from the horns of this vesicle as in the xiphidiocercariae. The main trunks do not divide but proceed to the cephalic extremity along the lateral margins. They sometimes receive small tributaries along their course. In the cephalic region the vessel commonly flexes back on itself. Such flexure may continue back to the posterior extremity of the body, as in *C. reflexae* (Cort, 1915, Fig. 43), or may continue caudad only a short distance, reflexing a second time (*C. biflexa*, Fig. 135). An intermediate form, *C. echinata*, has been described by Looss (1894:191), where the first flexure continues caudad while another part is reflexed cephalad.

A modification of the type represented by *C. biflexa*, where the double flexure is entirely within the cephalic region, is seen in *C. trisolenata* (Fig. 109). Either the end of the flexure has been fused to the most anterior part of the main vessel, or the middle portion of the system has been modified. As a result a triangular channel system has been formed at the anterior end of this excretory system.

The characteristic feature of the excretory system in the two species of echinostomes is the triplet of flame cells at the anterior part of the system. A detailed study of the flame cells in *C. biflexa* is found in figure 138. The cells are situated in the pockets communicating with the ultimate part of the reflexed tubule. Cell *a* is found in the sinus between the secondary and tertiary vessel. It points upward and outward. It is the smallest of the three cells. Cell *c* occupies the swollen end of the tertiary vessel. It is the largest of the three vessels; its cilia are the most rythmical of the group. Cell *b* lies midway between cells *a* and *c*. It points downward and inward. Cells *a* and *b* function in bringing the excretory wastes into the vessel from the surrounding tissue and cell *c* directs the excretory material along the vessel.

The excretory system of certain species of echinostome cercariae contain granules. These granules have been found in all *C. trisolenata* examined; they are found in the lateral vessels from the region of the pharynx posteriad to the acetabulum. They have not been seen in *C. biflexa*.

The excretory system in the tail of echinostome cercariae is not uniform. In *C. trisolenata* there is a single median tube with no prominent tributaries. In *C. biflexa* a median tube runs two-fifths the distance posteriad, where it divides to form two tubules which proceed distad. In *C. trivolvis* and *C. reflexae* (Cort, 1915, Figs. 39, 43) the median vessel of the tail courses backward about one-fifth way and ends there in a bifurcation, the ends of which

open to the sides. The *biflexa* type seems to be intermediate between the echinostome type described by Cort and the more common distome type. It is highly probable that the excretory system of the echinostome, with three flame cells in the anterior portion of the system and possibly several smaller ones further caudad, has arisen from the primitive distome type. In most cases, the posterior flame cells have become fused into larger ones, so that only three flame cells remain in the anterior part of the system in *C. trisolenata* and *C. biflexa.*

3. The Furcocercaria type. The mature apharyngeal distome cercaria of the furcocercous type (i.e. schistosome) has a very small bladder in the posterior part of the body and two lateral vessels running cephalad. The unpaired portion of the tail has a single median canal, which is united to the system of the trunk thru an "eyelet anastomosis." The median tubule of the tail forks to enter the rami. The origin of the caudal vessels has been worked out by Looss (1896, Figs. 172-174) for *C. vivax* Sonsino. These tubules arise as the posterior extension of the paired body excretory tubes. Their fusion in the common portion of the tail occurs after the rami have become well differentiated. The "eyelet" is an index of the original paired system in both body and tail.

A study of the species *C. gracillima* (Fig. 143) and *C. tuberistoma* (Fig. 155) shows the main features of the *vivax* type. The small bladder, the lateral canals, the median caudal tube, bifurcating distally to proceed into the rami, the "eyelet" at the junction of the body and the tail—all of these seem to be constant for the entire group. Beyond these characters the features of the several species are divergent.

In *C. gracillima* (Figs. 143, 145) the caudal portion is extremely simple, containing only the common median tubule and the forked tubule system entering the rami. Unlike *C. vivax* with its three pairs of flame cilia in the common caudal tubule, this species has no flame cells in the caudal portion of the worm. The system in the body of the cercaria has a non-muscular trilateral bladder, small posterior tubes arising from the lateral tubes, and a ciliary pocket about one-fourth way from the posterior margin of the body, on the inner wall of each lateral tube (Fig. 145). At the posterior margin of this ciliary pocket small tributary canals from the median plane flow into the main canal. Slightly cephalad is another pocket, somewhat larger than the ciliary pocket, filled with small granules of various sizes and shapes. Into this pocket four or five small canals empty, the median ones of which anstomose with their mates from the opposite side. No ciliary cells have been found in the terminations of the capillaries.

In *C. tuberistoma* the caudal portion of the worm is characterized by five transverse canals. Another pair, anterior to these, is conspicuous because it runs forward for a short distance and is then reflexed backward for some distance (Fig. 155). The eyelet and the bladder are both muscular. In the body portion there are no pockets for the lodgement of granules and no transverse anastomoses. No flame cells have been found in this larva.

A comparison of the furcocercous larvae with the Schistosomatidae shows the striking similarity of the excretory systems of these forms. Looss (1895) finds the system of male and female *Schistosoma haematobium* alike, altho that of the female may be slightly better developed, due to a minimization of the musculature. The bladder is median, non-muscular, except for a weak sphincter at the pore. It receives the two longitudinals at its antero-lateral reaches. There is no median canal (p. 72). Many of the laterals are dendritic, altho they do not anastomose. Small flame cilia are at the heads of the capillary tubes of 3μ to 4μ diameter. These flame cells and capillaries are intra-cellular, and not surrounded by an epithelial lining.

D. Excretory system of the Parthenitae. Details are given only in observations of Looss (1892:158-161) for the excretory system of young parthenitae. The "protonephridia" of Ssinitzin (1911:77-80; Pl. 1, Figs. 24, 25), described by him in connection with the birthpore of the redia, have not been proved to have an excretory function.

According to Looss the excretory sytem both in the sporocyst and redia arises as a paired structure, from which capillaries and flame cells soon arise. The observations of the writer have been confined to the adult sporocyst and redia of the species studied, in which the system is strikingly different from the embryonic condition. In many cases the excretory system consists of a diamond pattern of intercellular channels, without any clue to the former bilateral symmetry. The same amount of modification holds for both sporocyst and redia. Even in the holostome redia (Fig. 42) this diamond pattern is found. No flame cells have been found in adult parthenitae. This distinct modification of the excretory system in parthenitae is not surprising in view of the extraordinary degeneration of the animal that has resulted from its endoparasitic habits during its entire life.

Excretory granules. The excretory granules of the cercaria and parthenita are spheroidal and have the general appearance of glass beads. Their refractive index is very high. The size of the concretions is variable in different groups and even in the same individual. As a rule the granules are largest in the monostomes and holostomes.

Few writers have given consideration to these excretory granules. Thomas (1883:117) says for *Fasciola hepatica* larvae that "the yellowish granules. . . appear to be excretory products formed within the cells of the sporocyst and then ejected. They are partially soluble in acids, leaving an organic basis." Looss refers to them as opaque concrement-granules which on first sight throw the boundaries of the tubules into black relief (1894:165). They are insoluble in alcohol and color beautifully in stained mounts. Reference is made to these granules by Cort (1915:16) to the effect that the tubules of the monostomes are filled thruout their entire length "with small round concretions which disappear in the process of preservation." The writer has found that these granules are not usually preserved in the corrosive-acetic fixing fluids. However, if fixation is done without the acid fraction of the fluid the granules

are preserved. Application of strong acid to the granule causes an evolution of gas. The granules are negative to inorganic CO_2 tests, and are non-crystalline, as determined by the petrographic microscope. They take hematoxylin stains readily, altho they do not stain deeply. They give no Molisch reaction. The xanthroproteic test is positive, indicating a benzene nucleus. It is probable that they consist of a conjugate protein before fixation. Fixation with mercuric chlorid alters them, since they are then acid and alkali resistent.

Generalizations on the excretory sytem. The excretory system of the trematodes, including both cercariae and parthenitae, is essentially a bilateral system. It arises as two paired tubules, which fuse in the bladder region of the cercaria to form the vesicle. The mature system of the parthenitae is highly modified from the primitive type. The system as found in the cercaria is carried into the adult without very profound modification.

Most individuals of all generations contain within their excretory systems spheroidal concretions, which are waste organic products, quite probably derived proteins. They lodge in the main tubes and are expelled thru the excretory pore.

DIGESTIVE SYSTEM

The most uniform system in the Digenea is the digestive tract. With the exception of the sub-order Gasterostomata and the super-family Prostomata, the enteric canal is triclad in character. The main features of difference in the various families of the group is the modification of the esophagus region of the gut. In most forms there is a pharynx sphincter just within the oral pocket. In other species the pharynx is small and inconspicuous. In still others there is no bulbus around the esophagus, but in its stead a group of gland cells.

The digestive system in the cercaria is not distinctly a larval system but practically a fully matured system. In some cases it is not functional, as in the Monostomata, where the paired ceca are still filled with a jell (Fig. 13); in the Schistosomatidae there is the interesting phenomenon of short ceca in some species (*Cercaria gracillima*) and entire absence in others (*C. tuberistoma*). While the larval digestive glands of the cercaria may not be retained or may be metamorphosed in the mature worm, nevertheless they are functional in most larvae.

The forking of the ceca is not constant, varying in different species. Even the relative length of the parts of the tract varies greatly in the same individual at different times, due to the extreme limits of contraction and expansion of the larva, so that this relation of parts can not be entirely depended on as a basis for diagnosis. As a whole the digestive tract is remarkably uniform and simple, which might be expected in a larva in which the food supply is so accessible.

The sporocyst has no digestive tract, but takes its nourishment directly thru the body wall. In consequence the cells of the epidermis are thin and at times apparently glandular, as in the stylet cercariae.

The redia has a gut-pouch for a digestive system, with a pharynx sphincter around the anterior end. Hence the epidermis is not used in the capacity of food transference, and is heavily lined beneath with an integumentary secretion. For securing food the redia of *Cercaria pellucida* is provided with an oral piercing organ. The redia of *C. flabelliformis* is equipped with paired mucin-salivary glands.

GENITAL SYSTEM

This system of organs has been the most constant basis of classification of adult trematodes. It is also the best specific criterion for the larvae, altho a more delicate technic is required for differentiation of the genital organs in the cercaria than in the adult worm. Because these organs have failed to come out in the ordinary preparations, no attempts have been made to use them as basis for correlating larvae and adults. Cell masses have been figured by Looss (1896), Ssinitzin (1905, 1911) Miyairi and Suzuki (1914) and Cort (1915), but these workers have not in any case shown them in detail. By means of a lengthy staining in a weak solution of Delafield's hematoxylin, followed by rapid differentiation and then neutralization with potassium acetate solutions in the higher alcohols, the genital organs of the cercariae have been traced with a degree of detail not previously attained. These organs have been found to offer valuable data for correlating cercariae and adult trematodes.

A. Monostomata. All three species of monostomes on which observations have been made, *Cercaria pellucida*, *C. konadensis*, and *C. urbanensis* Cort are characterized by the symmetrically arranged testes, the presence of Laurer's canal, the location of the vitelline glands in a double series on each side of the body, and the courses of the uterus and vas deferens. Ssinitzin (1905, Fig. 76) shows the inner series of five paired vitellaria for *C. ephemera* Nitzsch, but he has figured no outer series of three glands, such as are found in the three species worked out by the writer. He is in error in considering them cystogenous glands, because their connection is traceable thru filiform ducts to the ootype. All these species are provisionally referred to the Notocotylidae. With the growth of the cercaria to the adult monostome the originally distinct and readily recognizable vitelline elements becomed fused in part. Looss's figure (1896, Fig. 94) of *Notocotyle verrucosa* (Froel.) shows five rather poorly defined foci of vitelline elements in each of the lateral series. It is possible that the five inner elements of the series have become fused to the three outer elements of the series, thus causing the indefinite outline of the elements in the adult worm. The vitelline glands of *Notocotyle quinqueseriale* are apparently eight to the side. Here the three glands of the outer series may have been introduced between the five glands of the inner series (Barker and Laughlin, 1911, Pl. 1, Fig. 10). A symmetrical pair of vitelline ducts, between the inner and outer series of glands, leads to the ootype.

The cercariae which the writer has studied in this group are readily distinguished by a comparison of their genital systems.

In *Cercaria pellucida* the well-developed cirrus pouch and the poorly developed vagina reach the confines of the excretory trunk just behind the median eye. In *C. konadensis* the cirrus pouch and the vagina are both equally developed. The former is falciform, the later pyriform. The vagina is lateral to the cirrus pouch but is somewhat posterior to it. The genital pore in *C. pellucida* is not as far posterior as that in *C. konadensis*. In this species, as well in *C. urbanensis*, the testes are marked by definite cell masses, while in *C. konadensis* the testicular masses are much more indefinite. They are small in each case and lie ventral to the vitelline organs. The course of the vasa efferentia is clearly outlined.

On the basis of the structure of the vitellaria alone these species can be differentiated in the cercaria stage. In *C. pellucida* the glands are actually spiculate in outline, flattened dorsoventrally. The vitelline material is finely granular and closely massed. In *C. konadensis* the glands are decidedly dendritic, and the granules are diffuse. In *C. urbanensis* the glands are lobate and the fine granules are included within a dense mucoid matrix.

B. Holostomata. The genitalia of the Holostomidae and Hemistomidae will be considered separately.

1. Holostomidae. The thickness of the tetracotyle larva, together with the thickness of the cysts, in which the majority of these individuals have been found, has prevented a study of the genital system from stained toto mounts. However, these organs come out clearly in frontal sections of 7μ thickness (Fig. 39). In *Cercaria flabelliformis* the ovary is situated just caudal to the posteriormost muscular lappet. A short oviduct proceeds dorsad to the ootype. The uterus winds posteriad to the genital pouch. The vitelline glands are long paired cords. In *C. flabelliformis* they are composed of large vesicular glands (Fig. 39); in *Tetracotyle pipientis* (Fig. 47) they are loosely follicular. The testes are paired structures which may occupy positions from the plane of the ovary (*T. pipientis*) to the plane of the genital pouch (*C. flabelliformis*). The pouch is muscular and opens posteriad, ventral to the excretory pore.

Thus these genital organs are typically holostome in character, corresponding to the main features described for the adults by Brandes (1891), Thoss (1897), and Johnston (1904). They are sufficiently detailed in this stage of the species development to be of diagnostic value.

2. Hemistomidae. In this family all of the genital organs are situated entirely posterior to the acetabulum. The primitive genital pore, anterior to the acetabulum, has lost its connection with the genitalia, and with the addition of muscular elements has assumed a suctorial function.

The species *Cercaria ptychocheilus* has an ovary elongate in a transverse plane, nearly spatulate, situated just behind the acetabulum. It is granulate, compact, and stains deeply with hematoxylin dyes. At its left it merges into the oviduct, a large coiled tubule, which bends on itself three times just behind the margin of the ovary, then empties into the ootype just anterior

to the bursa copulatrix. The densely massed cells of the glands in the vicinity of the ootype lie just above this organ. The testes are situated at the right side just ventral to the ovary. They are small compact glands, and have no ducts at this stage of development. The vitelline ducts from the diffuse vitelline follicles meet the other genital products in the ootype. The genital bursa is very large and muscular, and lies just ventral to the excretory bladder. Symmetrically arranged glands, with glandular nuclei and hyaline cytoplasm, empty into it from the postero-lateral reaches. They vary in number from seven to ten on each side.

With the exception of these glands emptying into the bursa, all of the genital organs of this larva lie in the anterior patelliform region. With the exception of the later formation of a uterine duct between the ootype and the bursa, all of the organs are in the approximate location where they will be in the adult worm. The massing of the organs in the anterior portion of the animal is undoubtedly correlated with the abbreviation of the appendicular portion of the species.

The literature on larval hemistomes (Diplostomulum) shows that von Nordmann (1832:34-35, Pl. III, Fig. 1) has described an egg pouch for *D. volvens* and two symmetrically arranged testes, with ducts, in the region of the acetabulum. Leidy (1904:111) describing *D. grande* (Diesing), speaks of "ovaries, dusky yellow." Since the ovary in the Holostomata is single, the organs thus described are possibly testes.

The bursa is the muscular organ *par excellence* in *Cercaria ptychocheilus*. Muscle elements protrude into the atrium, so that a constriction exists between the anterior and posterior portions of the organ.

The genital systems of the holostome and the hemistome are similar in those features in which they differ from the distomes. They have modified their primitive genital pore so that it has either become rudimentary or has assumed a muscular function. The sperm ducts and the uterine duct empty into the pouch at the posterior end of the animal, instead of the atrium anterior to the acetabulum. The new genital pore is posterior to the ootype, and ventral to the excretory pore.

C. Distomata. The genital organs of the distomes are different in various families.

1. Xiphidiocercariae. The genital organs in these cercariae are readily defined with reference to the acetabulum. They are mostly situated in the middle of the ventral side of the larva just behind the acetabulum or slightly posterior to this position. The ootype is posterior and dorsal to the acetabulum. The uterus coils around the right side of the acetabulum. It ends in a blunt or tapering cell mass. Laurer's canal is on the left of the median line, just behind the middle of the acetabulum. It is present in all of the species of stylet cercariae examined. Only in two species are the testicular cell masses outlined. In *C. crenata* (Fig. 59) these glands consist of two large ovate masses.

In *C. dendritica* (Fig. 86) the testes are small, situated closely behind the ootype. In no case is the ovary clearly differentiated from the region of the ootype.

The vitellaria are definitely outlined. These glands in *C. glandulosa* (Fig. 66), *C. diaphana* (Fig. 78), and *C. micropharynx* (Fig. 96) are much more alike than those in the remainder of the stylet species. The vitelline follicles of *C. dendritica* (Fig. 86), and *C. crenata* (Fig. 59) are noticeably dissimilar, having on the one hand, a system extending the entire length of the body, and, on the other hand, a system confined to the immediate vicinity of the ootype.

The genital organs and ducts of *C. racemosa*, the lateral fin type (Fig. 104), bear some resemblance to those of *C. dendritica* (Fig. 86). However, Laurer's canal is very prominent in this fintail species, while in *C. dendritica* it is not so prominent. Instead of coiling around the right side of the acetabulum, the uterus in *C. racemosa* makes four double oblique coils dorsal to the acetabulum. The ovarian cell mass is dorsal to the ootype and connects with that organ thru a short duct. The testes masses have not been observed.

2. Echinostomidae. The two species of this group which have been studied, *C. trisolenata* and *C. biflexa*, vary in the structure of their genital organs most markedly. In view of this diversity it does not seem advisable to take them up in detail in this comparative phase of the study.

3. Furcocercariae. The material of *Cercaria gracillima* was studied with especial reference to the genital cell masses, both in the totos and the section mounts. The main system consists of the ovary-uterus mass on the right and the cirrus mass on the left, both in the vicinity of the acetabulum. The vitellaria are lateral and empty into the ootype thru transverse ducts (Fig. 149). The testicular follicles are numerous, 24 or 25 having been counted. They are proliferated from a posterior germ mass, which is ventral to the bladder

NERVOUS SYSTEM

One of the earlier and better known system of the adult trematode was the nervous system. Leuckart (1863:462) states that Bojanus and Mehlis were familiar with the gross anatomy of the nervous system of the larger flukes, and that von Laurer, Diesing and Siebold as well as the elder van Beneden were acquainted with the nervous systems of both large and small worms. Leuckart described the sytem for *Fasciola hepatica* and *Dicrocoelium lanceatum*. He states that there are two or three stems, the anterior dorsalis and anterior lateralis and the thick posterior ventralis. Somewhat later Lang (1880: 46-50), substantiates the work of Leuckart and, in addition describes the dorsal posterior and acetabular innervation. Gaffron (1884) and Looss (1892, 1894, 1895) have placed the nerve anatomy of the adult trematode on a firm foundation. Hofmann (1899), Wright (1912), and Monticelli (1914) have confirmed the work of earlier workers. Nor has the finer work on the nerve endings and the ganglion cells been overlooked. Many of the earlier writers

made out the ganglion cells of the pharynx region and recorded their observations on the nuclei. Bettendorf (1897), working on *Fasciola hepatica* with intra vitam methylene blue and Golgi methods, has brought out clearly and convincingly the nervous sytem of this worm. This study has been augmented by the work of Zailer (1914).

In view of the extensive study of the nervous system of the adult trematode, it is a matter of no little surprise that so little has been done on the nervous structure of the cercaria and the parthenita. Looss (1894:245) has confessed the difficulty in making such a study and had observed that "ein, wie es scheint, nicht unbeträchtlicher Theil derselben fällt in die Zeit der Cercarienentwicklung, und weiterhin, ist auch der ganze Apparat während seiner Ausbildungzeit, dass es mitunter recht schwer ist, zu entscheiden was zu ihm und was zu dem umgebenden Parenchyme gehört." However, Looss depended on living mounts for his study and did not use preserved material or avail himself of intra vitam methylene blue technic. By the use of an eosin counterstain against a hematoxylin background the writer has been able to secure remarkably clear sections showing with extraordinary delicacy the nerve branches as well as the central nervous system. It is the purpose of this section of trematode morphology to present data and observations on the development and structure of the nervous system in parthenita and cercaria.

The central nervous system of the adult trematode consists of two central ganglion masses, situated dorsal and lateral to the pharynx and yoked together by a transverse commissure passing dorsal to the pharynx. The appearance of this structure has been aptly described by Lang (1880:46) as a saddle between oral sucker and pharynx. In cross section it is lunar. Here are centered the most of the ganglion cells, altho they are frequently found posteriorly, and often in the sensory apparatus of the oral and ventral suckers. The system also has a subesophageal commissure which differs in size and shape in different species of flukes. Extending forward into the region of the oral sucker are three pairs of nerve trunks, the dorsalis, lateralis, and ventralis. Of these three the latter is the most fully developed. It has a ramus muscularis which is both motor and sensory (Zailer), and an extensive connection with the oral nerve ring. The anterior lateralis is also a strongly developed trunk, with a ramus muscularis and a ramus palpalis, and transverse commissures to the anterior dorsalis and posterior lateralis. The anterior dorsalis is a weakly developed nerve which innervates the apical sensory field. A transverse commissure connects the two dorsales above the head muscle sheath. In addition to these three primary trunks, the palatinus, a weak motor nerve, lies internal to the anterior ventralis. Posterior to the central nervous system are the three posterior trunks, the dorsalis, lateralis, and ventralis. The ventral trunk is by far the most strongly developed. In addition to these is the small but conspicuous internal branch of the ventralis known as the pharyngealis. It occupies a posterior position, corresponding to the palatinus anterior to the central nervous system.

Braun (1893:683) considers the ventralis, dorsalis, and pharyngealis to be the three pairs of posterior nerves. However, the consistent course of the lateralis to the posterior extremity of the body, its early appearance in the embryology of the worm, and its commissural connections with the anterior lateralis and posterior dorsalis surely prove its right to a place in the rank of the primary posterior nerve trunks.

The nervous system of the monostomes has been worked out by Jägerskiöld (1891) for *Ogmogaster plicatus* (Crepl.), and by Monticelli and Looss for *Catatropis verrucosa* (Fröl.). Looss (1896:149) considers the system similar to the distome type. "Je n'hésité pas à attribuer au système nerveux de notre ver une construction analogue a celle que nous avons déjà signalée chez un bon nombre de Trématodes digénèses." However, Looss (1896:11-16) was not able to make out clearly the anterior trunks. Jägerskiöld (1891:14-16) describes the cerebral ganglion masses with the transverse commissure, the posterior ventralis, dorsalis, and lateralis, and the three anterior trunks, short and thorn-like, the homologs of the dorsalis, lateralis, and ventralis. A stem, designated as the "fourth," arising from the anterior reaches of the cerebral masses, passes ventrad to the region below the oral sucker; it seems probable that it is the palatinus. The only real modification from the distome type is the absence of the acetabular innervation, due to the loss of this organ.

In the Amphistomata adults among the earlier writers Lejtenyi (1881:142-144), working on *Gastrodiscus polymastos* Leuck., described two ganglion centra with the dorsal commissural bridge, but with only one anterior and one posterior pair of trunks. In contrast to this incomplete description is that given by Looss (1896:21, 22) for *Gastrodiscus aegyptiacus* (Cobb), where the usual distome nerve trunks were found, and, in addition, a median anterior and a median posterior nerve. Looss has worked out the nerve anatomy for *Amphistomum subclavatum* Rud. in even greater detail (1892:151; Taf. 19, Figs. 1, 2,), and finds that they correspond to the distome type, except for the innervation of the posterior sucker.

The one group of the Digenea where the nervous system has been almost entirely neglected is the Holostomata. Brandes (1891) states that none of the workers of the nervous system up to his day have worked on the holostomids. He has observed only the central nerve center lying above the posterior portion of the pharynx, an anterior and a posterior pair of nerve trunks, the tracings of which he has found in sections. Thoss (1897), working on *Holostomum cucullus*, finds the main nerve center lying dorsal to the origin of the esophagus, with two pairs of anterior and one pair of posterior nerve trunks.

The central nervous system of *Cercaria trisolenata*, the echinostome, consists of two masses of ganglion cells and the dorsal commissure lying concavely on the dorsal side of the large muscular pharynx. The commissure is broad and flat. The dorsal surface of the ganglion masses and the commissure present a smoothly curved surface, but on the ventral side the ganglia bulge out against the pharynx. The anterior trunks consist of the dorsalis, lateralis, ventralis, and the palatinus. The paired dorsales arise together with the

laterales and proceed forward with them for some distance. After separation, the dorsalis runs more median, then flexes outward and dorsalward over the oral hood, proceeding toward the apical sensory center. The lateralis at the point where it leaves the dorsalis proceeds outward and forward, so that it reaches a level slightly below the plane of the central nervous system. Slightly after diverging from the dorsalis the lateralis gives back a commissure to the dorsalis. This dorsolateral connective fuses with the dorsalis just behind the posteriormost branching of this trunk. Arising from the most ventral reaches of the ganglion center is the ventralis, a broad flat trunk, which courses outward and downward to the oral lip of the oral sucker. Internally it gives off the palatine, which lies just lateral to the pharynx.

Caudal to the central nervous system arise the four pairs of posterior trunks, the dorsales, the laterales, the ventrales, and the pharyngeales. The dorsalis branch arises dorsal and slightly lateral to the junction of the ganglion and the commissure. It runs straight backward, slightly dorsal to the plane of the central nervous system. The lateralis arises slightly lateral to the dorsalis; its path lies outward and backward. The ventralis arises from the very heart of the ganglion mass. It spreads outward and then runs backward parallel to its mate. The ventral commissure, arises just median to the origin of the posterior ventralis flexing below the prepharyngeal opening. It is stout and bowed considerably downward. Between the commissure and the ventralis arises the pharyngealis.

In a germ ball of *Cercaria trisolenata* some 45μ by 60μ in size, the central nervous system is well developed. This may be called the *butterfly stage* (Fig. 121). At this period there are two pairs of main trunks anterior and four pairs posterior to the central ganglion mass. The anterior trunks are the ventrales and the laterales. By reference to the next stage in the development (Fig. 122), the dorsales are found to arise from the sinus between the laterales buds of figure 121. They arise at first as a single bud and bifurcate later. Caudally the most conspicuous trunks are the dorsales, which arise in a median plane and conspicuously dorsal to the other posterior trunks. The dorsal commissure at this period is practically negligible. The outermost ventral trunk-buds are the laterales, short and stubby at this period of growth. The ventral trunks arise from the ventral portion of the cerebral masses. Between them and the laterales arise trunks which are present in the embryonic stage only. They may be designated as the posterior intermedius nerves.

In stage II (Fig. 122) a very decided change has occurred in the outline of the central nervous system, altho the fundaments of the first stage described are present. Anteriorly the intermediate space between the laterales has disappeared and from that region has arisen a wedge which is the fundament of the paired dorsales. The ventral trunks have been set off to themselves by a lateral growth and elongation of the intermediate fibers. On the caudal side of the ganglion the posterior dorsalis has been separated from its mate by the growth of the dorsal saddle commissure. Most noticeable, however, is the

change that has taken place in the ventral portion of the system. Here the space between the ventrales has become exceptionally wide and a prominent commissure has grown out from the trunks, commonly known as the subesophageal commissure. It is the homolog of the transverse commissure occuring along the entire ventral side. The intermedius trunk has become fused with the posterior lateralis, in part, and then crosses over to the ventralis. This is the connection known in adult nerve anatomy as the ventrolateral commissure, a strong and important intercommunicating trunk (Fig. 123). In the developmental stages no trace of palatinus or pharyngealis has been found.

Cercaria glandulosa, a xiphidiocercaria, is favorable material for the study of the minute structure of the nerve fibers and endings. In the anterior end of this larva there occur in five frontal sections of 8μ thickness all of the fundamental nerve endings of this region. In section 1 of the worm (the most dorsal section), there are no nerve structures save a few sensillae to the dorsal lip of the oral sucker. They receive innervation from the anterior dorsalis, and derive that innervation from the anteriormost fibers seen beneath in section 2, just in front of the musculus preoralis. Section 2 (Fig. 68) shows the trunk of the dorsalis descending into the oral musculature. It has three main branches, one coursing to the preoral region to supply the conductive strands for the preoral sensory endings, one becoming the short superficalis, and a longer one, the profundus, passing under the endings of the superficialis. In the region of the musculus preoralis, the apical sensory field is continuous across the sucker from right to left. In section 3 (Fig. 69) are illustrated the main outlines of the central nervous sytem, together with the anterior trunks. Here is the dorsal portion of the ganglion cells. Anterior and dorsal is the dorsal commissure and ventral is the subesophageal commissure. The forward traces are the trunks of the laterales with the outermost superficial ramus palpalis and the more deeply situated ramus muscularis. The latter branch innervates the musculus preoralis and the anterior lip of the oral sucker. On the left is the trunk of the anterior ventralis, arising from below the mass of the ganglion cells. At the anterior extremity is the apical sensory field. The dorsolateral commissure is very clearly shown in this section. Section 4 (Fig. 70) shows the remainder of the central ganglia with the left anterior ventralis passing forward. This is a large trunk, with an especially important ramus palpalis leading to the apical sensory field, and a small oral nervus communicans supplying the oral nerve ring. This ring completely encircles the superficial region of the oral sucker and connects with the superficial branch of the dorsalis. The ramus muscularis of the ventralis and the palatine branch of the ventralis are found in section 5 (not figured).

Passing caudad all the posterior roots are well defined. Four posterior roots are visible in section 3 (Fig. 69). These include the posterior dorsales, laterales, ventrales, and pharyngeales. In a fortunately cut section of the same species the innervation of the acetabulum is beautifully demonstrated (Fig. 71). The two main longitudinal trunks, the ventrales and the laterales,

are connected by commissures. Those around the acetabulum are of especial importance. The preacetabular commissure arises from the lateral trunk and proceeds in a posterior oblique course, then around the anterior reach of the acetabulum to meet the branch from the other side. The postacetabular branch arises from the lateralis also, but continues caudad along the course of the ventralis. Behind the acetabulum it meets the branch from the opposite side to form the span. From these trunks circumscribing the acetabulum two ring commissures arise, a superficialis and a profundus, of which the latter with the nerve endings is found in the section (Fig. 71).

The nervous system of the monostome, as worked out by Jägerskiöld (1891, Taf. I) for *Ogmogaster plicatus* (Crepl.), has been substantiated for the most part in the study of *Cercaria pellucida* (see figure 23). The three paired posterior trunks are evident. The posterior ventralis is the most important of these and can be traced to the caudal extremity of the animal in all cercariae of this species, as well as in *C. konadensis* and *C. urbanensis*. The dorsalis is less conspicuous, yet it is usually traceable far caudad. The posterior lateralis is delicate. It arises near the origin of the ventralis and swings out laterad in a great bow. It, too, can usually be traced to the posterior extremity of the body.

The anterior trunks can also be definitely traced. The ventralis arises from the extreme lateral horn of the ganglion center in conjunction with the posterior ventralis. More median, the anterior lateralis is found. The two anterior dorsales arise as a single structure along the median line. Their primary function in the cercaria is the innervation of the median pigment eye, altho branches may be traced farther anteriad. Likewise, an important branch of each posterior dorsalis constitutes the nerve tract to the lateral eye.

The ganglion cells in the monostomes are superficial to the nerve strands. A considerable number of them are not even in intimate contact with the fibers, but have fibrillar communications with them. The ganglion masses from which the nerves arise are distinctly cornuate, with a wide dorsal commissure.

Pigmentation and eye-spots in the monostomes. The monostome cercariae that have come under the direct observation of the writer, together with those described in the literature, may be placed in two groups according to their eye-spots, namely, those with a single pair of eye-spots, disposed laterally to the brain center, and those with an additional median eye, anterior to the central nervous system. The amount of pigmentation is considerably larger in the trioculate species than in the binoculate type. Figures 1 to 3 show in dorsal view a series of stages in the pigmentation of *Cercaria pellucida*. The pigment originates anteriorly over the brain center and proceeds caudad along six lines of growth. A very careful study of the pigmentation in these species indicates that a very simple but reasonable relation exists between the pigmentation and the underlying nervous system. The pigmentation is found to be a delicate superficial index of the underlying nerve fibers. This

pigmentation is present in the subintegumentary areas and follows with precision all the ramifications even to the nerve endings. Figure 37 shows the nerve endings in the anterolateral reaches of *Cercaria pellucida*.

In the paired eye-spot a definite subspherical "lens" is found in the region of the concentration of the pigment. In the median eye of the trioculate type a "lens" is sometimes present. The origin of the eye is simple. At an early stage in the germ ball (60 μ to 80 μ), when the cell masses of the nerve trunks are definitely outlined as they emerge from the ganglion center (Fig. 36), a branch of the posterior dorsalis, larger than any other nerve, pushes out obliquely. It meets an invagination of the ectodermal layer, which may be considered an "optic cup." There soon forms in the hollow of the cup a group of dark brown refractory granules, which entirely lines the optic cup several layers deep and leave but a small cavity within. The optic branch of the dorsalis bends back into the cavity at the place where it first comes in contact with the cup and here ends in a pyriform enlargement, the nerve cell. The structure of this end organ is such that it might be interpreted as a "lens," if the connection with the nerve is not made out. Cort (1915:15) has placed that sort of an interpretation on the eye structure of *C. urbanensis* and *C. inhabilis*. For the former he states that "each true eye is formed by a mass of pigment in the form of a cup, the bottom of which is thicker than the sides. A lens fits into the opening of the cup, leaving a space between its lower surface and the bottom of the cup." And again, for *C. inhabilis*, "the large eyespots . . . are composed of the lens and the cone of pigment like those already described for the monostome, *Cercaria urbanensis*." The writer has studied some of Cort's material and has found sections where such an interpretation might be made from a single section. But in the preceding or following section the connection of this "lens" with the optic nerve is plainly seen.

The eye structure as studied in this monostome is similar to that found in the Monogenea, especially the type in the posterior eye of *Tristomum molae* (Hesse, 1897:559; Taf. 28, Fig. 29).

The nervous system of the monogenetic trematode was first studied in detail by Lang (1880), who made out the pigment cup, a refractory body (lichtbrechender Körper), a ganglion cell, the retina, and eye muscles (p. 41; Taf. I, Fig. 2, Taf. II, Fig. 2). Most later investigators mention only the perceptory body and the accessory apparatus, altho André (1910:217) has identified the muscle fibers of Lang. The writer believes that the movement of the eyes depends largely on the general bodily movement.

In the adult Monogenea studied the pigment cup is found to lie between the refractory bulb of the eye and the possible source of light (Goto, 1894:81). In the monostomes, as in *Dendrocoelium lacteum* (Hesse, 1897, Taf. 27, Fig. 10), the hollow of the cup is directed outward, so that light falling on the eye must pass thru the end organ before reaching the inner portion of the pigment complex.

The pigment of the organism is probably the waste product in the metabolic economy of the worm. Its close association with the nerve endings in the

monostome cercariae seems to indicate that it is the melanoidin fraction of the oxidative processes in the nervous system. The possibility of utility as a receptor of light or heat is a secondary item and must not be confused with the primary meaning of the pigmentation.

In the free-living Platyhelminthes the fully developed eye is present in the mature individual. In the ectoparasitic trematodes the eye-spot is well developed in the young animal (Hesse, 1897:560, 561), but degeneration takes place as the animal matures. Goto (1894:81), speaking of Tristomum, observes: "Morphologically speaking they are certainly degenerate eyes; and have probably been derived from such eyes as are found in Turbellaria; but I do not think they are functional. In the first place the pigment granules are situated on the dorsal side and thus prevent the light from reaching the lens, since the dorsal side is the only direction from which light can come. In the second place there is not always a distinct retina. If these 'eyes' are really still useful to the animal, they may possibly be a temperature sense organ; and for that purpose their structure seems to answer well." Goto goes on to show that the more degenerate condition of the eyes in *Tristomum ovale* is due to the greater degree of internal parasitism of this species than that of *Tristomum molae*. In the monostome, the eyes are well developed in the cercaria but become fully degenerate, with a loss of all the pigment in the adult, so that the adult of one species has been described by Creplin as "albidus" (Jägerskiöld, 1891:4). In some species of Allocreadiidae (*Crepidostomum farionis* O. F. M. and *C. cornutum* (Osborn)), pigment eye-spots are found in the adult. A still further stage of degeneracy is found in *Cercaria racemosa* (Fig. 100) and *C. gracillima* (Fig. 144), where the optic nerve is still present but the pigmentation is absent.

In *Cercaria gracillima*, the representative of the furcocercariae, the nervous system is narrow, in correspondence with the attenuate condition of the animal. The posterior laterales are not found in the mature cercariae, altho the bud is present in the germ ball (Fig. 151). One is struck by the significant resemblance of the main nerve complex of this cercaria and that of *Schistosoma haematobium*, described in detail by Looss (1895). The three pairs of anterior trunks are readily made out, altho, in addition, a prominent dorsolateralis is found (Fig. 150). The posterior dorsalis arises from the dorsal side of the ganglion cell mass and proceeds caudad to the region of the acetabulum, where it fuses with the ventral trunk. A prominent subesophageal commissure and a small pharyngealis are present. The fundamental resemblance between the system described for this cercaria and that for the schistosome adult seems to the writer to be sufficient morphological evidence for the correlation of these apharyngeal furcocercariae with the Schistosomatidae.

A study of the nervous system of the Holostomata has been made of *Cercaria ptychocheilus*, based on both toto mounts and sections (Fig. 53). No adequate idea of the nervous system of this group can be secured from the meager data of Brandes (1891) and Thoss (1897). The dorsal commissure is

indistinct and thoroly fused with the ganglion masses. The latter are wide, with a construction in each in the region of the origin of the lateral trunks. The trunks figured by Thoss are probably the ventrales, since they supply the main innervation of the animal. The anterior ventralis arises along with the posterior ventralis just anterior to the latter. The anterior trunk soon divides. The major portion runs around the oral sucker, while the external branch is traceable anterolaterad. The anterior lateralis is represented by a blunt stock just outside the pharynx. It runs cephalad but soon ends in two delicate branches. There is no posterior dorsal of posterior lateral. The posterior ventral is stout and thick. It gives off one prominent branch externally soon after it reaches its most external position. At regular intervals it gives off branches internally which have the indication of rudiments of commissures. These transverse trunks just anterior and posterior to the acetabulum are still well developed; they are similar to those described for the distome.

Contrary to the opinion of Looss (1894:245, 246), the writer has found without exception that the general trematode nerve anatomy can be traced from the early germ balls up thru various stages of growth, and that the cercaria shows not only the potentialities of the adult system, but actually the details of this system. Moreover, the study of various groups of cercariae has demonstrated that the fundamental deviations and modifications from type are recognizable in the mature cercaria. Thus this study has shown that the nervous system of the cercaria is constant for the group to which it belongs, and is a definite basis for the natural classification of the groups.

In contrast to the highly developed nervous system found in the cercaria is that of the parthenita. In the sporocyst no definite nerve complex is found, altho Looss (1892) has observed nerve elements in miracidia of *Amphistomum subclavatum*. In the redia, however, with the continued functioning of the highly muscular pharynx, there is a nerve complex practically embracing the entire anterior portion of the gut (Fig. 125). Viewed from the dorsal, ventral, or lateral aspect, the system in surface view appears as an H. It is resolvable into four anterior trunks, four posterior trunks, and a ring commissure. On the dorsal side are two swellings, the rudiments of the cerebral ganglion masses of the cercaria. The nerve cells of the system are very prominent. They are usually bipolar or multipolar (Fig. 126), but, as might be expected, the more superficial ones are more often the multipolar cells.

This redia nervous system constitutes a very primitive type, in which the nerve cells are much more frequently diffuse and more discrete than in the systems in the cercariae. It is probable that the pharynx is responsible for keeping the system from total degeneration.

The size, number, and location of the ganglion cells vary according to individual species of cercariae. They may be situated within the ganglion centers, as in *Cercaria micropharynx* (Fig. 97) and *C. glandulosa* (Figs. 69, 70); they

may be scattered around the ganglia altho not imbedded in the fibers. In the redia of *C. trisolenata* the fibers are less conspicuous than the ganglion cells. Species closely related may have cells of different numbers and different sizes. In *C. micropharynx* there are always just two ganglion cells, imbedded in the fibers, just above the esophagus. Their nuclei are large, pyriform, and usually containing conspicuous refractory nucleoli. They measure 5.5μ to 6μ in short diameter by 8.5μ to 9μ in long diameter. The nucleoli are about 2μ in diameter. *Cercaria glandulosa* presents a case where there is a definite number of minute ganglion cells within the ganglion masses. There are fifteen cells in each of the two masses. The cell walls are not well defined, but the nuclei are readily distinguished. They measure 1μ to 1.5μ in short diameter by 1.5μ to 2μ in long diameter. The ganglion cells of *C. pellucida* are numerous; it has not been ascertained whether they are constant in number. They are subspherical at times, but are usually multipolar. The entire cell averages 3.3μ by 6μ while the nuclei measure 1μ to 1.6μ. The cells of the redia of C. *trisolenata* are usually multipolar in the region of the epidermis. They range from 6μ to 22μ in diameter. The nuclei are inconstant in size, varying from 2μ to 6μ in diameter. The nuclei of the ganglion cells of *C. gracillima* are so minute in the nerve complex in the germ balls (Fig. 151) that they are barely visible under 1,000 magnification. Yet these nuclei are definitely set off from the surrounding matrix. They measure about 0.4μ in diameter.

In cell-studies of adult trematodes the nerve cells have been measured in many cases. The measurements range from 80μ (Lejtenyi, 1881:41) in *Gastrodiscus polymastos* to 6μ (Fischer, 1883:17) in *Opisthotrema cochleare.* The nuclei range from 12μ (Juel, 1889:41) in *Hemiurus excisus* to 1.6μ in *Opisthotrema cochleare* (Fisher). A comparison of these measurements in adult trematodes with those for the cercariae, shows that the nuclei of the adult cercariae are as large as those of the adult trematode. It is evident, however, that the cells are much smaller in the cercariae. Ageing of these cells consists, then, in the growth of the cytoplasm rather than an increase in size of the nucleus.

DESCRIPTION OF THE TREMATODES INFECTING MOLLUSKS OF THE BITTER ROOT VALLEY

INTRODUCTION

On account of the biological isolation of the Bitter Root Valley, it is little wonder that it contributes new species of trematodes. The fourteen species of trematodes found in the valley are not thot to comprise the entire trematode fauna of the region, but are the representative species for the year and season when the study was made. Of the fourteen species found in the Bitter Root River, two are larval Monostomata, two are Holostomata, and the remaining ten are Distomata. In addition to these, a larval holostome, *Tetracotyle pipientis* nov. spec., from the vicinity of Chicago, Illinois, is included in the study for the sake of comparison.

Previous to the writers' preliminary report (Faust 1917) the following larval trematodes have been described for North America.

MONOSTOMATA

Cercaria hyalocauda Haldemann 1842
Glenocercaria lucania Leidy 1877
Cercaria urbanensis Cort 1914

AMPHISTOMATA

Cercaria inhabilis Cort 1914
Cercaria diastropha Cort 1914
Cercaria gorgonocephala Ward 1916

DISTOMATA

Cercaria agilis Leidy 1858
Rhopalocerca tardigrada Leidy 1858
Gymnocephala ascoidea Leidy 1877
Cercaria platyura Leidy 1890
Cercaria reflexae Cort 1914
Cercaria megalura Cort 1914
Cercaria leptacantha Cort 1914
Cercaria caryi Cort 1914
Cercaria isocotylea Cort 1914
Cercaria brevicaeca Cort 1914

DISTOMATA

Cercaria polyadena Cort 1914
Cercaria hemilophura Cort 1914
Cercaria trigonura Cort 1914
Cercaria trivolvis Cort 1914
Cercaria rubra Cort 1914
Cercaria douthitti Cort 1914
Cercaria wrightii Ward 1916
Cercaria anchoroides Ward 1916
Cercaria marcianae La Rue 1917 (Really a *Distomulum*)
Cercaria vergrandis La Rue 1917 (Really a *Distomulum*)

HOLOSTOMATA

Diplostomulum cuticula (v. Nordmann 1832)
Diplostomulum grande (Diesing 1850)
Diplostomulum volvens (v. Nordmann 1832)
Tetracotyle typica (Diesing 1858)
Diplostomulum parvulum (Stafford 1904)

Cercariacum

Cercariaeum helicis (Leidy 1847) Later recorded by Leidy as *C. vagans* (1850).

In addition, there is the doubtful form, *Cercaria bilineata* Haldemann 1840.

According to Stiles and Hassall (1908:157), Leidy is credited with the record of a species, *Diplostomulum rhachiaeum* (Henle). Investigation of the literature shows this to be an error, owing to the confusion of the names Leidy and Leydig. Fr. Leydig described the species *D. rhachiaeum* for Europe in 1853 (Leydig, 1853:383).

Of the thirty-two forms listed, it is doubtful if any except those described by Cort (1914), Ward (1916) and LaRue (1917) could be recognized by their descriptions, since in the majority of cases the data are so indefinite as to leave the systematist a wide range of choice in determining the species. An excellent

example of this valueless type of description is afforded in the form *Diplostomulum cuticula* (von Nordmann 1832), reported by four American investigators from various localities east of the Rocky Mountains. The descriptions include larvae encysted with pigment and without it, some specimens found subdermally, others taken from the peritoneum of the body cavity, all secured from a great variety of teleost fishes. In none of the descriptions is there mention of the course of the excretory system or of the genital cell masses, both of which are essential to the exact determination of the species. It seems reasonably certain that a careful revision of these forms described as *Diplostomulum cuticula* (von Nordmann) would result in the discovery of several new species of Diplostomulum.

The species of cercariae and parthenitae described in this section of the paper have been studied with special reference to the excretory, genital, and nervous systems.

MONOSTOMATA

Cercaria pellucida Faust 1917

This larval trematode is a muscular cercaria, characterized by heavy anterior pigmentation on the dorsal surface, centered around three foci, the paired lateral eye-spots and the median eye. It is a member of the trioculate group of the Monostomata. The pigmentation tends to spread caudad from the pigment center along six lines of growth, two dorsal, two lateral and two ventral. These lines of pigment have been shown (p. 53) to be the superficial index of the underlying nerve trunks. The worm is characterized by 1) a transparent body, 2) a circuit of refractory granules that marks the excretory system, 3) a small oral sucker, and 4) large longitudinal muscle bundles of the tail.

Cercaria pellucida was obtained from *Lymnaea proxima* Lea in the Bitter Root River in the vicinity of Corvallis, Montana, and from *Physa gyrina* Say near Buckhouse Bridge. The snails were examined in October, 1916. *Lymnaea proxima* contained a heavy infection with this species, along with a lesser infection with the monostome cercaria, *C. konadensis*, and a distome larva, *C. diaphana*. Physa was heavily infected with an echinostome, *C. trisolenata*, and contained only a light infection with the monostome. In all cases the infected organs were the liver ceca.

The mature *C. pellucida* has an average measurement of 0.4 mm. to 0.7 mm. in length and 0.18 mm. to 0.2 mm. in width. The tail is about 0.5 mm. long and has a diameter of 0.07 mm. at the base. Most usually the animal has an elliptical constricted outline, such as is shown in figure 4, but when relaxed it assumes the elongate-ovoid or spatulate condition, shown in figures 1 to 3.

The parthenita is a large conspicuous redia, measuring 2.2 mm. by 0.5 mm. (Fig. 6). Within the redia is a large rhabdocoel gut extending almost the entire length of the animal and measuring 0.3 mm. in cross section. The gut empties anteriad thru a muscular bulbus 15μ in length and 12μ in cross sec-

tion. It is spinose internally (Fig. 20). In the prepharynx region is a unique piercing organ (Fig. 17), probably of ectodermal origin. It is four-lobed and is covered with spines. A rythmic eversion of the organ against the host tissue and redrawal within the pharynx region of the parthenita is a characteristic movement of the redia. Around the muscular pharynx is a ganglion mass consisting of a fibrous matrix and a network of ganglion cells. Behind the head region is a neck-like constriction, and behind the neck is a sacculate body. At the extreme posterior end is a large papilla. The redia is covered with a non-cellular basement membrane, and imbedded in this superficially in the form of minute tuberosities are the remains of the epidermal nuclei (Fig. 22).

The walls of the redia are well-supplied with muscular layers, longitudinal and transverse, so that the parthenita is capable of extraordinary distension and contraction, altho it has no specific locomotor organs.

The germ balls of the redia arise from the matured ova, derived from four cells localized at the posterior extremity of the parthenita. Altho the cells lying next to the wall around this quartet may be potentially germ cells, they take no part in the ordinary proliferation of germ cells (Fig. 22). From these cells arise the germ balls, thru cleavage into 2, 3 and 5 cells, after which certain cells of the ball appear much smaller than the others and grow over the latter, giving rise to the gastrula by epiboly. The young germ balls usually lie en masse behind the gut, while the more advanced cercariae are crowded anteriorly. They appear strangely grotesque, with their pigment eyes and their snout-like bodies oscillating back and forth within the body wall of the parthenita.

Aside from the larger size of the body and the trioculate anterior end, *Cercaria pellucida* might be at first confused with *Cercaria urbanensis* Cort. While the size and eye-spots are sufficient to separate these two species, a more careful examination shows that there has not been a separation of two species at all, but more correctly two groups of species. The group of smaller species is binoculate and ranges around 0.3 mm. to 0.46 mm. in length by 0.1 mm. to 0.16 mm. in width, while the group of larger species is trioculate and averages around 0.5 mm. in length by 0.15 mm. to 0.2 mm. in width. Consequently from a description of external characters alone there is no means of separating *Glenocercaria lucania* Leidy from the Bitter Root species *Cercaria pellucida*. It is such a problem as this that has caused the writer to believe that there are characters more deeply seated in the larva that will readily set it off from others of the same group.

Sufficient care in technic makes it possible to bring out very clearly and convincingly the genital organs of the Bitter Root species. Here are characters, constant both in the larva and the adult that readily differentiate these monostome cercariae. These have been described in detail in the section devoted to morphology (p. 45) and need only to be summarized at this point. The median ovary just in front of the excretory bladder opens out thru a short duct at its left (Fig. 18), and after receiving the common vitelline duct, opens

anteriad into the uterus. This organ has an outlet just behind the median eye. It ends in a poorly developed vagina. No Laurer's canal has been definitely made out in the totos but there is evidence of such an organ in sections. From the sides and slightly caudad to the ovary the closely massed testes open into filiform vasa efferentia which unite anterior to the ovary to form the vas deferens. This canal is directed forward parallel to the uterus, ending in a bulbous cirrus pouch just to the left of the vagina. The three paired outer vitelline follicular masses and the five paired inner masses occupy a dorsal position. They are irregular in contour (Fig. 4), with aciculate margins, and are finely granular with close massing of the granules. Inconspicuous common vitelline ducts connect the vitellaria with the ootype just dorsal to the ovary.

The excretory trunks are similar to those of the entire group of monostomes. The bladder is quite small, 48μ in section, moderately muscular, superficially triangular, with the excretory pore posterior. The excretory tube in the tail is vesicular at the base and narrows down distad (Fig. 4). The tubes of the trunk are crowded with large excretory granules.

The digestive system is typically triclad, with ceca extending to the subdistal extremity. They are filled with a jell, and are crowded with granules imbedded in the jell. No pharynx has been observed. The oral sucker is directed ventrad. It is small but powerful.

The parenchyma is filled with cystogenous granules, included in one-celled cystogenous glands, probably of mesodermal origin (Fig. 14). Between the cystogenous cells are angular parenchyma cells, more commonly known as vesicular cells (Blasenzellen), with processes extending to the integument and possibly functioning in the capacity of secretory ducts for the basement membrane.

The locomotor organs at the posterior angles of the trunk are neither spiculate nor spinose. They possess no cement glands. The tail has no central pair of gland elements such as are found in binoculate cercariae of the monostome group. However, the ordinary parenchyma cells of the tail of *C. pellucida* are remarkably large and vesicular and suggest a glandular function (Fig. 19.).

Large isolated bands of transverse muscle fibers are present thruout the body just within the basement membrane. Longitudinal muscles are not so large in the trunk as are the transverse series, but constitute the important muscle system of the tail. The transverse muscles of the tail frequently give a moniliform appearance to that organ, such as is described by Leidy (1877) for *Glenocercaria lucania.*

The nervous system of *C. pellucida* (Fig. 23) varies from the distome nervous system only in its relation to pigmentation and the eye-spots. There are six anterior trunks and six posterior trunks arising from a paired brain center. They constitute the dorsal, lateral and ventral nerve lines. These trunks are carefully followed by the melanoidin pigment fraction. The eye-spots receive

innervation from the dorsal trunks; the paired eyes are innervated from the posterior trunks and the median eye from the fused branch of the anterior dorsales. The optic nerve runs forward from its origin in the dorsalis and enters the pigment cup from above, ending in a sensory cell (Fig. 24). The general anatomy and histology of this eye-spot is similar to that described for all Turbellaria and Monogenea. However, no previous account has been found for the structure of the eye-spot of the Digenea showing its relation to the central nervous system.

Locomotion is brought about thru a coöperation of the body musculature together with the special functioning of the oral sucker and the posterior locomotor pockets. The tail serves as a swimming organ, with a peculiarly rapid and nervous lashing.

Encystment occurs as a final step in the larval stage of the life-history of the hermaphroditic generation, in preparation for entering the definitive host. The process is rapid and the mucoid cyst is secreted by the cystogenous glands before the tail has been thrown off. This organ is freed from the cyst by the violent wriggling which it produces. The cyst is spherical; it encloses the now quiescent larva. The outer portion of the cyst is an opaque mucoid, which gives the cyst an appearance of a white grain, about the size of a pin-head. The larva now waits transfer to the definitive host.

Cercaria konadensis Faust 1917

Cercaria konadensis is a species of monostome cercaria of the binoculate type. The species is more graceful than *C. pellucida*. Its bodily contour is most usually spatulate, while the long tail reaches far behind. The small amount of pigmentation around the two eye-spots and the less usual pigmentation along the nerve trunks caudad serve to indicate the superficial differences between the binoculate group to which this form belongs and the trioculate group.

Cercaria konadensis was found in *Lymnaea proxima* Lea, collected from the Bitter Root River at Corvallis Montana in October 1916. It occurred as an infection along with the larger species, *C. pellucida*. Of the snails examined, 31.3 per cent were infected with this cercaria in the connective tissue between the liver ceca. The cercaria measures 0.4 mm. to 0.46 mm. in length and has a bodily width of 0.1 mm. to 0.16 mm. (Fig. 25). The tail is of equal length under conditions of relaxation, but may be extended so as to exceed by far the bodily length. At its base it has a transverse diameter of 30μ to 40μ. The posterior locomotor organs are not so conspicuously lateral as those of *C. pellucida* (Fig. 4). Considered together with the younger stage of *C. pellucida* (Fig. 12), these pockets suggest an origin from the caudal pockets found in certain distome cercariae. Unlike those of *C. pellucida*, the posterior locomotor pockets of *C. konadensis* are provided with about ten gland cells surrounding the lumen, cells probably of a secretory nature (Fig. 21).

The parthenita (Fig. 26) is a relatively small, elongate redia, 1.7 mm. in length and 0.35 mm. in transverse section near the middle. It is attenuately obtruncate, with the posterior end sloping down to a blunt point. The pharynx is muscular but small, 60μ in cross section, and aspinose internally (Fig. 31). The rhabdocoel gut extends posteriad about three-fifths the body length. The posterior end is filled with cells, composed of a central rachis with apex directed posteriad, and an outer cell complex of goblet cells (Fig. 30). The central rachis comprises the germinal epithelium, the proliferating region of which is situated subterminally. From this epithelial mass the matured parthenogenetic eggs are proliferated forward so that the germ balls come to lie in the lumen posterior to the gut. Similarly to those in *C. pellucida*, only the maturing cercariae come to lie around the gut.

The excretory system of *C. konadensis* consists of the circuitous trunk system, opening posteriorly into a non-muscular vesicular bladder. This vesicle measures 16μ to 17μ in width and 14μ to 15μ along the longitudinal axis of the cercaria. The excretory pore is dorsal, opening from the middle of the bladder (Fig. 29).

The digestive system is of the usual triclad type, with no distinct pharyngeal region.

The genital organs are notocotylid in character, but different in several features from those of *C. pellucida*. The ovary (Fig. 28) is skull-cap shaped, with a distinct Laurer's canal. A short oviduct leads into the ootype. The uterus, emerging from the ootype, runs cephalad, ending in a swollen vagina some distance behind the line joining the paired eye-spots. The vitellaria consist of a double series of five inner and three outer follicular masses. The individual glands are very diffuse and dendritic.

The testes are small, lateral, and posterior to the ovary, with the vasa efferentia describing a broad crescent anteriad around the ovary and meeting in a common tube, the vas deferens, which runs forward to the left and parallel to the uterus. The vas deferens ends in a swollen cirrus pouch (Fig. 25).

The nervous system corresponds to the monostome type described for *C. pellucida*, except that the dorsal trunk to the median pigment eye-spot is lacking.

In the tail six paired groups of gland cells, derived from parenchyma, occupy places just lateral to the median canal of the excretory system, each group dove-tailing into the one next proximal. These caudal glands indicate a much closer kinship of this worm to *Cercaria urbanensis* than to *C. pellucida*.

Encystment is brought about by the pouring out of the contents of the cystogenous cells and by subsequent decaudation.

HOLOSTOMATA

Cercaria flabelliformis Faust 1917

Cercaria flabelliformis is the first larval holostomid to be described in detail for North America. Leidy has listed *Tetracotyle typica* Diesing from

Lymnaea catascopium and *Physa heterostropha* (1890). Rettger (1897) has mentioned a larval tetracotyle in connection with a life-history study, but he has failed to identify the species.

Cercaria flabelliformis was found in three collections of *Physa gyrina* Say, taken from the Bitter Root River in the vicinity of Corvallis, Montana, in October 1916. Practically every snail from these collections bore evidence of infection with the parthenita of this species, altho only 14.7 per cent of the snails examined contained the tetracotyle. The mature cercaria has a length of 0.48 mm. to 0.56 mm., and a width of 0.44 mm. It is about 0.2 mm. thick. While the anterior end is not clearly set off from the posterior end as is usual in holostomids, it does have the suctorial cup which includes all the ventral suctorial apparatus, including among the rest the lateral suctorial grooves. In the young larva these lateral organs are discoidal (Fig. 41); in the mature tetracotyle they have become modified into lateral lappets (Fig. 40).

The larva was found maturing within the redia, free in the liver interstices, and encysted in the liver tissues. It was seldom found free in the tissues.

The parthenita (Fig. 42) is a redia which measures 0.5 mm. in length by 0.052 mm. in transverse section. The head is set off from the trunk by a collar prominence, while in the posterior third of the body are found the "walking feet," which protrude ventrolaterad to support the redia. The posterior end of the body is produced into a large knob, in which are parenchyma and germinal epithelium cells. At the oral end is a wide muscular organ. It is not clear whether it is a pharynx or an oral sucker. It is about 40μ in transsection and surrounds the fore-end of a gut 0.18 mm. long. On the ventral side are two groups of salivary glands, six cells to each group, opening into the anterior region of the gut thru a common duct for each group (Fig. 43). Around the anterior end of the gut, just behind the muscular organ, is a nerve complex (Fig. 42), differentiated into two ganglion masses on the dorsal side, four nerve trunks, and a circumintestinal commissure. A birth-pore is here ventral and slightly sinistral. The wall of the parthenita is heavily covered with an integument of non-cellular material, beneath which are muscle and parenchyma elements. Running thru the parenchyma is a complex diamond-pattern excretory system.

The germinal epithelium is localized at the posterior end of the redia. It offers an unusually fine opportunity for study of the maturation of the ova. The detailed description of this maturation is found in the section on morphology (p. 16).

The germ balls may differentiate into a second generation of rediae and cercariae at the same time. These larvae are about equal in size as they develop, but the cercariae differentiate much more rapidly than do the rediae so that the two are readily distinguished. Usually only three or four cercariae are found developing at one time in the redia, along with many daughter rediae. This fact seems to indicate that the animals have come to depend largely on parthenogenetic propagation. The cercariae escape thru the birth-pore and

soon encyst in the free tissue of the host. The second generation redia is already producing germ balls before it comes to take up a free existence outside the first generation redia.

The internal systems of organs of *Cercaria flabelliformis* are of considerable interest. However, since they are described in detail in the respective sections in the morphological division of this paper (pp. 37, 45, 54) they will not be treated here.

Valuable data on holostomid anatomy are obtained by a comparison of *Cercaria flabelliformis* with the following species:

Tetracotyle pipientis nov. spec.

This species of larval trematode was found in March 1917 in the mesentery and pericardium of a large number of *Rana pipiens* collected in the vicinity of Chicago, Illinois. All of the frogs were more or less infected with this holostome. The infection consisted of creamy oval yellow cysts, either single or in grape-like clumps. Each cyst consisted of many lamellae, and innermost, a tough cyst membrane. The inner membrane stains a deep brown with iodine in 70 per cent ethyl alcohol. The gross measurement of the cyst ranges from 0.5 mm. to 0.76 mm. in lesser diameter and 0.7 mm. to 1.0 mm. in greater diameter, while the inner membrane is about 0.3 mm. by 0.5 mm. Within the inner membrane is the larva, tightly coiled at one end of the cavity, while the remainder of the cyst, often two-thirds of the volume, is filled with accumulations of large excretory granules. Some of these granules have fused to form single clumps as large as the larva

When the lamellae and cyst membrane are teased open and the larva is allowed to work its way out, the body becomes expanded and flattened. It then measures 0.5 mm. in length by 0.37 mm. in trans-section (Fig. 47). The oral sucker is 75μ in diameter. It lies in an anterior cone of the body. Antero-lateral prominences and the blunt posterior portion of the body give a lyrate outline to the worm. The primitive genital pore, 80μ in diameter, lies in a plane where the anterior and posterior portions of the body join, just within the suctorial pocket. The free ventral wall of this pocket is often folded backward so that it fits down snugly against the body. At other times it bulges out so that the pocket cavity is a large ovoid atrium. The acetabulum is represented by a single lappet situated behind the primitive genital pore. The non-muscular accessory suctorial grooves consist of long narrow slits, directed obliquely inward toward the acetabulum. The entire worm is covered with minute anterior and posterior spines, equally prominent. The primitive genital pore is crowned with a ring of fused spines. The lateral suctorial organs are surrounded by a band of discrete spines imbedded in the tissues.

The worms examined were all filled with excretory granules. A careful study of the larva showed the main course of the excretory trunks to appear as shown in figure 48. The median posterior excretory pore, slightly dorsal, communicates with the bladder which merges imperceptibly with the paired

lateral trunks. These tubes lie just within the margins of the larva and unite with one another in a large transverse vessel at the anterior end of the body, so that a complete circuit is formed. If a rent is produced in the body near the oral sucker, it is customary for the excretory granules to be poured out there rather than thru the natural channel. A tube from the lateral trunks crosses thru the ventral pocket wall at its anterior end. Tributary tubules, bisymmetrically arranged, empty into the main trunks, mostly at the anterior and posterior margins of the body.

The digestive tract is simple and inconspicuous. A small swelling within the oral sucker marks the pharynx, just behind which is the esophagus. The ceca barely clasp the anterior margin of the primitive genital pore.

The genital organs are readily recognized as holostome in type (Fig. 47). They open posteriad. A small spherical ovary lies median. Dorsal to this is the ootype, into which come the short oviduct and the transverse vitelline ducts. The vitellaria are diffuse bands of large follicles extending from the anterior face of the acetabulum to the posterior margin of the genital pouch. They lie strictly ventral. Two large oval testes lie to the sides of the ovary, the one (t_1) slightly anterior to the other (t_2). They have individual ducts (efferent) which reach the genital pouch and fuse into a common vas deferens just before entering the genital pouch. This organ is muscular, oval in contour, with the transverse diameter longer than the longitudinal.

A survey of the literature shows that only one tetracotyle has been reported for Amphibia, *Tetracotyle crystallina* (Rud.), from the mesentery cysts in *Rana temporaria*, *R. esculanta*, *Bufo igneus*, *B. viridis*, and *Vipera berus* (Rudolphi, 1819:380-382). The formation of the cysts is not clearly described, but the large size of the Europen tetracotyle, together with its oval contour, aspinose body and oval accessory sucking discs, clearly separates it from *Tetracotyle pipientis*. The new species conforms much more to the type represented by *T. colubri* v. Linstow, but differs from it in the relative sizes of the oral and ventral suckers, and the possession of small spines all over the body instead of a few broad spines (Linstow, 1877:192; Fig. 22).

While the excretory system is one of the best systems of organs to use in systematic work with trematode larvae, in the absence of such data for other tetracotyles described, the comparative data actually afforded are sufficient in this case to justify the establishment of *Tetracotyle pipientis* as a distinct species.

Observations on the anatomy of *Tetracotyle pipientis* present an opportunity for comparison with *Cercaria flabelliformis*, the parasite of the Bitter Root mollusk, *Physa gyrina*.

The two larvae are about equal in length, but *C. flabelliformis* is considerably the wider. The widest region in *T. pipientis* is in the anterior region of the body; the widest portion of *C. flabelliformis* is in the middle of the body. The suctorial pocket in the former species has grown over the ventral surface so that a true pocket is formed with the opening anterior; in the latter

species the suctorial pocket is hemispherical with the opening ventral. The lateral accessory suctorial grooves in *T. pipientis* are non-muscular oblique slits; in *C. flabelliformis* they are at first oval depressions which are modified later into a pair of lateral lappets. The primitive genital pore in *C. flabelliformis* is 0.05 mm. in diameter; in *T. pipientis* it is 0.08 mm. wide, with a crown of heavy spines. The homologies between the lateral excretory trunks of the two species are apparent, altho the median transverse trunk is much farther anterior in *T. pipientis* than in *C. flabelliformis*. The tributary tubules are entirely different in the two species. The digestive ceca of the Bitter Root species conform to the family type in extending well into the posterior part of the body; those of *T. pipientis* are short and rudimentary. The genital organs of the two species occupy the same relative position, altho individual variations in size and shape of organs are evident.

In concluding the study of the tetracotyle larvae, emphasis must be placed on the maturation of the parthenogenetic ova, which shows that these larvae do not develop in miracidia, without the intercalation of parthenitae as Brandes (1891:572) and Fantham (1916:224) believe. This fact, previously recorded by the writer (1917), makes the morphological evidence complete in support of the view of true alternations of hermaphroditic and parthenogenetic generations among Holostomata.

Cercaria ptychocheilus Faust 1917

This form, really a Diplostomulum, is elongate ovate in outline, with dorsoventral flattening, slight ventral concavity, and a more or less distinct separation of body into anterior and posterior portions. In addition, the group to which this worm belongs lacks the lateral auxiliary sucking grooves which are characteristic of the tetracotyle forms. Several species of Diplostomulum have been well described and their excretory system beautifully traced by von Nordmann (1832). These include the species *D. volvens, D. cuticula, D. clavatum*, and D. *brevicaudatum*. Of the forms found in North America there have been recorded *D. cuticula*, *D. volvens*, and *D. grande* of the Old World species, and *D. parvulum* (Stafford), new to North America. However, as has been previously suggested, none of these American records give sufficient data to distinguish accurately the species.

The general outline of the body of *Cercaria ptychocheilus* is such as to distinguish it readily from the described species. Broadly oblong-ovoid in contour, with the anterior half laminate and the posterior portion fleshy, this cercaria might at first be confused with distome cercariae. Such a confusion is caused, further, by the abbreviated appendiculate portion of the larva, which, on extension into a caudal cone, may reach one-third of the body length, but on contraction barely protrudes behind the anterior part of the body. The concavity of the anterior part is found only in the fleshy region behind the acetabulum. Here in this area is found the muscular complex comparable to the cup-shaped suctorial apparatus of the tetracotyle.

The Diplostomulum (Fig. 49) measures 0.48 mm. to 0.63 mm. in length by 0.17 mm. to 0.37 mm. in width, and about 30μ thick in the fleshly portion of the body. The oral sucker is small but powerful, and is directed strictly anteriad. Behind this oral region the esophagus is enlarged into the pharynx, about 40μ in section. Behind the pharynx is an equal portion of the esophagus which is non-muscular, posterior to which the ceca rise, spreading out into a broad furculum.

The acetabulum is large and circular; it is situated somewhat posterior to the middle of the body. At times of extreme contraction the acetabulum becomes narrowed antero-posteriorly, with a transverse wrinkling. This disc measures 70μ in diameter. The primitive genital pore, situated just in front of the acetabulum, has lost its connection with the genital system and has become modified into a muscular sucking disc.

The excretory, genital, and nervous systems have been treated on pages 37, 45, 54, as types for the hemistome larva. A comparison of these data with v. Nordmann's observations on *Diplostomulum cuticula*, *D. volvens*, and *D. clavatum*, and with the work of Blanchard (1847) on *Hemistomum alatum* (Goeze) shows the fundamental conformities and differences of the excretory systems of the group. However, the nervous system (Fig. 53) is worked out thoroly in this paper for the first time in the Hemistomidae. The genitalia bear a fundamental resemblance to those of the adult species, as described by Brandes (1891), but differ in size, shape and position of the respective organs. This difference may be accounted for in part by the immaturity of some of the organs, but there are undoubtedly specific differences, such as the lamellae of muscular nature in the genital pouch and the glandular cells emptying into the pouch.

The larva *Cercaria ptychocheilus* was taken from mesentery cysts of *Ptychocheilus oregonensis* Richardson, caught in the Bitter Root River in April 1915 in the vicinity of Stevensville, and Carlton, Montana. Thousands of cysts were found. The cysts are much larger than the larvae (Figs. 50, 51) and are filled with a limpid milky fluid which bathes the larva and serves as a liquid cushion. The cyst is oblong, and flattened. It is composed of a thin, tough membrane, and it is attached to the mesentery by a discoid annulus in the middle of one of the flattened sides. Within the cyst the worm works around and grows, so that it comes to fill the cyst in later life. At frequent intervals there is extruded from the excretory bladder a considerable quantity of granules which pile up at the posterior end of the larva within the cyst, but are soon dissolved and absorbed by the fluid medium.

The encysted animal when placed in a normal saline solution soon increases its activity and bursts thru the cyst. This rent usually occurs at one end of the membrane. The larva then crawls out with a "measuring worm movement." After several hours of activity it settles down on the bottom of the container and remains quiescent, altho slight mechanical disturbances activate

it again. In a modified Ringer's solution ninety per cent of these larvae were kept alive for forty-eight hours.

It seems probable that *Cercaria ptychocheilus* is in an intercalated host.

DISTOMATA

Xiphidiocercariae (Stylet Larvae)

The xiphidiocercariae are grouped together because of their possession in common of a larval stylet. The writer believes that the features of the genital and excretory systems of the group are more fundamental characters which will hold the members of the group together.

Cercaria crenata Faust 1917

Cercaria crenata is a delicate larva, with an ovate bodily outline and a short lanceolate tail (Fig. 55). The body measures 0.25 mm. in length by 0.13 mm. in width, and the tail, 0.15 mm. to 0.16 mm. in length by 20μ to 30μ at the base. The entire body except the tail is covered with minute hair-like spines. A large median spine, the stylet organ (Figs. 56, 57) lies in the dorsal wall of the oral hood. This organ is about 30μ long by 5μ in width at its base. It has the general shape of a quill pen, with reinforcements at its base and also in the distal portion toward the acute point. The distal third of the stylet is bent ventrad about 20 degrees. There are two prominences in the anterior portion of this organ, one where the shaft joins the quill and a less prominent one-half way between this position and the quill point.

The oral sucker is relatively large, 20μ in diameter, while the acetabulum, situated three-fifths the way from the anterior end, measures just half that diameter. The tail is inserted in the posterior caudal pocket which has no spinous projections.

Cercaria crenata was found in large numbers in 13.6 per cent of *Lymnaea proxima* Lea, taken from the springs at Fort Missoula, Montana, in October 1916. It occurs in oval sporocyst sacs, 0.5 mm. in length and 0.35 mm. in diameter. At one end the germinal epithelium, is localized and from this end the ova are proliferated. Only cercariae have been found to develop within the sporocysts.

When the cercaria is mature its breaks thru the wall of the sporocyst and swims thru the surrounding medium. The tail is retained for a considerable time, and encystment is slow. This seems to indicate a considerable period of free-swimming life.

The internal structure of *Cercaria crenata* is such as to distinguish it readily from the other stylet cercariae. The excretory system is characterized posteriorly by a subspherical vesicle, deeply crenate. It measures 20μ long and 30μ wide. Anterior to the bladder a bicornuate trunk empties into the vesicle thru a common median tube. The horns of the U are widely separated. At the place where each main lateral turns forward there is given off a small dendritic tubule, directed posteriad. Some distance ahead of the acetabulum

the main lateral trunk divides into inner and outer tubes, each of which has a number of branches and capillaries. The main tube of the tail is median, with no prominent tubules.

The digestive system consists of an esophagus provided with a pharynx for most of its way, and, behind the pharynx, a typical gut extending to the posterior plane of the acetabulum.

The salivary-mucin glands in *C. crenata* are of a unique type. An outer series of eight small vesicular cells, with a common duct system into the oral pocket, corresponds to the usual salivary-mucin gland system of cercariae. These glands are readily made out in the living worm. An inner series of five cells, two of which are just behind the pharynx and three behind the acetabulum, empty thru a common duct system into the oral pocket. This series is not seen in the living larva, but in stained specimens the cells show small vesicular nuclei with deeply staining cytoplasm and numerous chromophilic granules. This inner series probably consists of a type of salivary gland different histologically and suggests a correspondingly different function.

The genital cell masses are prominent and are well differentiated early in development. Their structure and position are indicated in figure 59. The ovary lies posterior to the acetabulum and median whereas Laurer's canal lies anterior and to the left. The uterus is characterized by a double coil, which ends in a moderate sized vagina, just anterior to the acetabulum. The vitellaria are limited to three cords which lie in a transverse plane just posterior to the ovary. The large flask-shaped testes lie behind the ovary. This genital system suggests the Plagiorchiine arrangement. The distribution of vitellaria is similar to that described by Poirier for *Plagiorchis sauromates* (1886, pl. 2).

Cercaria glandulosa Faust 1917

A stylet cercaria characterized by a multiplicity of glands has received the name of *Cercaria glandulosa*. It is somewhat larger than *C. crenata*, is more oblong-ovate, and is a much more active larva (Fig. 60). The body measures 0.45 mm. in length and 0.2 mm. in width. The tail is slightly shorter than the body, 0.35 mm. in length, by 50μ to 60μ in section at the base. The tail is set within the caudal pocket. This pocket is provided with a pair of locomotor grooves, in which are set a number of stiff spines. Below the insertion of the tail is a small lappet (Fig. 63), provided with three spines directed posteriad. A mucoid secretion is present in the sinuses of the pocket, lateral to the base of the tail.

The stylet organ measures 39μ in length by 5μ in width at the base of the shank. It is reinforced all thru, but especially at the base of the shank, and thruout the quill. The point of the stylet is blunt. The stylet, as well as the entire body, is very delicate, and is shattered by the slightest pressure of the cover slip. The oral sucker is directed downward; it measures 86μ in diameter, while the acetabulum, in the middle of the ventral side, is smaller, with a diameter of 66μ.

The cercaria was found in the liver tissues of *Physa gyrina* Say from the Bitter Root River in the vicinity of Hamilton, Montana, in October 1916. Forty per cent of the physas examined were infected with the parasite. The cercaria develops within a very simple sporocyst, which has a length of 0.34 mm. and a width of 0.17 mm. (Fig. 67). The wall of the sporocyst is delicate, consisting of a single layer of very thin epidermal cells, with no basement membrane and no muscular complement. The genital epithelium is localized at one end, and from this only a few cercariae are developed at any one time.

The excretory system of *Cercaria glandulosa* presents some interesting features. The bladder is flattened, truncate, and subterminal instead of terminal. A narrow canal communicates with the excretory pore which is median posterior. The four angles of the bladder are muscular. When the bladder is emptied these corners lie close together, so that the cavity of the bladder is small. Then by the expansion of the bladder this organ is filled from the trunks (Figs. 64, 65). Two vesicular cornua empty into the bladder. Each cornu is directed laterad and slightly anteriad; it soon constricts to form the lateral tube. The common tube divides soon to form the posterior tubule and the anterior tube. The anterior vessel then divides in the region of the acetabulum to form a trifurcate system. Just behind the region of this division there is a small vesicular swelling where granules of the system accumulate. The excretory system in the tail consists of the common median vessel and several tributaries.

The digestive system is characterized by an abundance of glands, so that the entire tract is surrounded with gland cells. A small pharynx surrounds the esophagus near the anterior end of the tube. The esophagus extends to the preacetabular region, at which place it forks to form short furcae which barely clasp the anterior end of the acetabulum. Along this entire course there are many gland cells in clusters, especially abundant in the pharynx region. Their relation to the pharynx and nerve ganglia is shown in figure 72. The individual gland cell is ovate, with a short neck. The cytoplasm is chromophilous. There is no recognizable duct connection thru the myoblasts of the pharynx to the lumen. The nuclei of these cells are large and studded with granules.

In addition to the grape-like clusters of gland cells surrounding the entire digestive tract there are right and left paired gland groups of the salivary-mucin type. They consist of nine large cells to each group, usually situated in the acetabular region, but capable of extension, so that they may lie as far caudad as the bladder (Fig. 62). Figures 73 and 74 show sections passing thru the anterior tip of the excretory vesicle. In each of these a right and a left gland are visible. In these glands not only is the nucleus granular, but the cytoplasm is densely granular, the granules being assembled in little clumps. Frequently (Fig. 73) there are vacuoles within the cytoplasm.

The genital organs are represented by cell masses which show clearly the location of the mature organs, but as yet show little differentiation (Fig.

66). Ovary, Laurer's canal, vagina, uterus—all are recognized in the midacetabular region, with vitelline follicles extending from the oral aperture to the posterior end. They are divided into anterior and posterior portions. No testes are yet to be found. The genital organs as a whole seem to indicate Plagiorchid relationship.

Conspicuous thruout the body are the large bundles of longitudinal muscle fibers. They are scattered thruout the parenchyma at the anterior end (Fig. 72), while they are much larger and more concentrated laterad in the region of the acetabulum. Still further caudad they become fewer and less conspicuous (Fig. 74).

The nervous system has been described in detail on page 51.

This cercaria lives a free-swimming existence for only a short time. When placed in a watch-glass in tap water, it soon drops its tail, preparatory to encystment. The tail is helpful in locomotion, yet after decaudation this species is more active and able to cover considerably more ground than most other species with the aid of the tail. This movement is due in no small measure to the spines in the locomotor grooves of the caudal pockets. After moving about for a little while the cercaria settles down and pours out an abundance of slime within which it coils up and becomes quiescent until a transfer to the new host is effected.

Cercaria diaphana Faust 1917

Cerceria diaphana is closely related to *C. glandulosa*. When contracted, it is broadly ovate (Fig. 78), but on extension it assumes an elongate ovoid contour (Fig. 76). The measurement of the body when at rest is 0.2 mm. to 0.26 mm. in length by 0.1 mm. to 0.12 mm. in width. Under pressure of a cover slip the internal organs are beautifully worked out and the delicate mist of the parenchyma in which they are imbedded suggests the term "diaphanous." The tail is broadly lanceolate, 0.15 mm. in length by 0.04 mm. at the base. It is inserted into a caudal pocket provided with spinose locomotor pocket grooves. The spines are few in number (8 to 10) and well developed. They are directed meso-caudad. As in *C. glandulosa* the two sinuses of the caudal pocket are thickened by a mucoid lamination. The acetabulum is situated in the middle of the ventral side; it has a diameter of about 32μ. The larger and more powerful oral sucker has a diameter of 44μ. The stylet organ (Fig. 77) is a delicate but firm quill of 39μ length and 5μ width at the base of the shank. It is entirely without any reinforcement in the region of the shank but has thin ventral plates at the junction of the shank and quill, while inserted in the quill point, directed posteriad, is a minute spine, 5μ long and 0.5μ in diameter.

Cercaria diaphana was found in the liver tissues of *Lymnaea proxima* in the Bitter Root River near Corvallis in October 1916. The infection was heavy. The cercaria develops in an oblong sporocyst (Fig. 79), frequently drawn out or contorted at one end (Fig. 80). The unique feature of the

sporocyst is that the germinal epithelium is not localized; consequently germ balls may be derived from any portion of the body. Whether or not the germ cells arise parthenogenetically has yet to be determined. This type of germ ball production represents a structural simplicity previously not recorded for the sporocyst.

The excretory system differs from that of other stylet cercariae mainly in the shape of the bladder and of the essential tubes. The bladder is small, heavily muscular, flattened antero-posteriad. Leading out from it in a median plane is a non-muscular shank of some length, which opens into two cornua a considerable distance in front of the bladder. Caudad these cornua are vesicular, but further cephalad they become constricted into a system of tubules similar to those of *C. glandulosa*, which run thru the body to collect the excretory wastes.

The digestive system consists of a long esophagus, with pharynx at the anterior end, and a wide bifurcation somewhat anterior to the acetabulum. The entire digestive tract is very attenuate in outline. It is not supplied with glands along the furcae but has an even more abundant supply than *C. glandulosa* in the region of the pharynx (Fig. 76). Altho the pharynx itself measures only 15μ in cross section, the glandular area as a whole embraces a sphere 65μ in diameter. The rest of the tract is free from gland cells of this nature. The salivary-mucin glands are situated in the upper outer reaches of the furcae. Each group consists of eight cells, relatively very small, granular, with a common duct system opening into the oral pocket.

The genital organs are similar to those of *C. glandulosa* (Fig. 78). They differ from the genital cell masses of that form in the more limited vitellaria, and the more conspicuous Laurer's canal. This form is probably a Plagiorchid larva.

Unlike *C. glandulosa* this cercaria is slow to drop its tail and much slower to encyst, in spite of the fact that there is an equally good pair of posterior locomotor pockets with spines and an equally good supply of cystogenous material. We have here, then, evidence of a physiological adaptation to different conditions of the environment, where the structure of the two types would lead one to expect similar habits and reactions.

Cercaria dendritica Faust 1917

Cercaria dendritica is a species of cercariae readily recognized by its obovate structure, large suckers, large muscular pharynx, and large muscular excretory vesicle. The body as a whole is heavily muscular. The tail is short and almost conical (Fig. 81). The body measures 0.33 mm. to 0.4 mm. in length by 0.13 mm. to 0.17 mm. in width. The tail is about half the body length, 0.16 mm. and is 0.04 mm. wide at the base. It is inserted into a typical caudal pocket, the whole cavity of which is lined with stiff spines. The large oral and ventral suckers are nearly equal in size. The former has a diameter of 62μ and the latter of 60μ. The stylet (Figs. 82, 83) is short and stout, heavily reinforced at the shank, with a flat deltoid quill. The quill

is pointed at the tip. It is directed ventrad by about ten degrees more than the shank. The stylet has a length of 44μ and a breadth at the base of the shank of 14μ.

Cercaria dendritica was secured from two collections of *Lymnaea proxima* taken from the chara sloughs at Fort Missoula, Montana, in October 1916. The infection was in the liver interstices. The parthenita (Figs. 87-89) is a well-developed sporocyst, with an attachment disc, but without any indication of a digestive tract. It seems to approach a redia more nearly in its structure than any other described sporocyst. The sporocyst is muscular and heavily covered with integument. The parthenogenetic eggs develop from a germinal epithelium situated at the antipodal end from the disc. The stages of cleavage are clearly made out from the study of the germ cells proliferating from the germinal epithelium (Fig. 89). This layer is closely pressed against the epidermis. As the cells mature they increase in size. The increase continues thruout the cleavage, so that a three-cell stage is larger than a one-cell stage, and a morula is larger than a five-cell stage. This continued growth of the embryo is accounted for by the nourishing medium which bathes the sporocyst. This is a special case of nurture, where the growth stimulus is reacted to immediately. The germ ball attains a considerable size before it begins to differentiate, altho epiboly has occurred soon after the morula stage has been reached. The animal is mature before it breaks thru the wall of the sporocyst and swims out into the inter-cecal spaces.

The larva has an interesting excretory system (Fig. 81). An immense spheroid bladder, somewhat crenate, opens dorso-posteriad thru a small pore. Anterior it receives the contents of two large muscular cornua thru a common opening. These cornua extend laterad to the extreme margin of the animal. At the outside of each, at the margin of the worm, arise three tubes, one directed posteriad and two directed anteriad. The capillaries are dendritic. The caudal tube is a median canal without any prominent tubules.

The alimentary system consists of a pharynx with muscular fibers developed early. It has a width of 30μ and a length in section of 36μ. A short, attenuate esophagus opens posteriad into two vestigial furcae. Anterior and lateral to the acetabulum are the salivary-mucin glands, eight to each group. They are moderately large (Fig. 85), and empty thru common duct systems into the oral pocket.

The conspicuous features of the genital system (Fig. 86) are the large swollen vagina, and the prominent Laurer's canal, the latter extending out on the left side of the acetabulum under its posterior margin. In the mid-area, just behind the acetabulum, are two small pyriform testes. The vitelline glands extend from the extreme anterior margin of the worm to the extreme posterior end; they are attenuate, sparsely branching serpentine chords, composed of a long anterior and a short posterior portion. The vitelline ducts run in from the postero-lateral regions to the ootype, which is just anterior to the testes. This type is suggestive of Plagiorchid relationships.

Soon after the cercaria is set free into the water, it drops its tail. Almost before the observer is aware it secretes a thin membrane from the abundance of cystogenous material contained in the large cyst cells which pack the parenchyma of the worm. The oval cyst with the worm coiled up inside is shown in figure 84. This type of cyst offers only a temporary lodgement for the cercaria, and it is evident that the worm must reach the definitive host soon if the infection is to be successful.

Cercaria micropharynx Faust 1917

Cercaria micropharynx is a minute larva of the xiphidiocercariae, oval in contour, with small clavate tail (Fig. 93). The body is covered with minute spines arranged in diamond pattern, progressively less prominent toward the caudal end. The spines are probably constant characters of the adult as well as of the larva, since the entire trunk is well supplied with these spines while the tail is naked. The body measures 0.18 mm. in length and 0.09 mm. in width. The tail is 0.14 mm. long and 0.03 mm. at the base. It is inserted into a caudal pocket provided with a group of spines on the lateral lappets ventral to the tail. The oral sucker is large for the body size, 35μ in diameter, while the acetabulum is slightly smaller, 30μ in diameter. Inserted in the hood of the oral sucker is the stylet organ (Figs. 91, 92), 34μ long and 5μ to 6μ in breadth along the shaft. The organ is reinforced all around and has a velum stretched across the ventral surface of the quill.

The cercaria was secured from the infected liver tissues of a large number of *Lymnaea proxima*, taken from Rattlesnake Creek, Missoula, in November 1916 and in May 1917. The cercariae develop in oval irregular sporocysts, measuring 0.24 mm. along the long axis and 0.18 mm. along the short axis (Fig. 94). The body wall of the sporocyst consists of a single layer of epidermal cells, between which are found numerous excretory granules, lying in irregular grooved channels. There is no localization of the germinal epithelium, so that germ balls arise from all portions of the body wall and, when mature, break out into the body lumen. Not only do the cercariae develop to maturity in the sporocyst, but in some cases they drop their tails and encyst in the sporocyst (Fig. 95). Thus the larval host, the snail, is the food of the intercalated or of the definitive host, since no free-living stage is commonly found. In case the cercaria is pressed out of the sporocyst before encystment, it swims about for a very brief period, then drops the tail and encysts.

The excretory system consists of a subspherical vesicle and bellows-shaped cornua, which open into the vesicle thru a common cylinder. The three usual tubes of the excretory system are present, the single posterior and the two anterior ones. The tail tube is single median, with a few inconspicuous lateral tributaries. The cornua are filled with excretory fluids; they are lined with cells (Fig. 98).

The digestive system consists of the very minute pharynx in the midregion of the esophagus, and two vesicular furcae considerably anterior to the

acetabulum. No glands occur in the pharynx or cecal regions, but in the prepharynx region, just within the oral aperture, is a band of about fifty goblet cells of a glandular nature. The salivary-mucin glands are found at the sides of the acetabulum. They consist of eight cells for each group. They are relatively large, vesicular, and have common ducts opening into the oral pocket. In addition to the usual transverse and longitudinal systems just within the integument (Fig. 97, 98), large muscle elements are scattered thruout the parenchyma.

The genital organs (Fig. 96) consist of a prominent vagina, a well-defined Laurer's canal, and a group of massed organs in the vicinity of the ootype. In addition, there are the yolk follicles, distributed over a wide range of the dorsal side of the animal. The follicles are closely massed together. This species suggests a Plagiorchid genital system.

Cercaria racemosa Faust 1917

Cercaria racemosa belongs to that group of stylet cercariae usually designated as *cercariae ornatae*, by virtue of their possession of a fin-fold structure to the tail. While this separation may be concomitant with a deeper, more fundamental difference of type, it is well to bear in mind that fin-folds occur in other groups, such as in monostomes, *Cercaria lophocerca* (Filippi, 1857:5; Fig. 3), echinostomes, *Cercaria echinatoides* Fil. (La Valette:1855,Taf. I, C), and among the furcocercous larvae, *Cercaria cristata* (La Valette, 1855,Taf. II, K). It may be looked on as a modification of the caudal organ for swimming.

The body of *Cercaria racemosa* is elongate ovoid, measuring 0.29 mm. in length by 0.11 mm. in width (Fig. 100). It is characteristically broadest just ahead of the acetabulum. The tail consists of a central lanceolate region and a lateral ruffled fringe, which is most conspicuous at the distal end. The tail measures 0.22 mm. in length and 0.04 mm. in width at the base. It is inserted into the posterior extremity of the trunk, altho there are no lateral sinuses to be found in this caudal pocket. The acetabulum is slightly caudal to the middle of the body. It measures 26μ in diameter, while the larger oral sucker has a diameter of 36μ. The stylet organ (Figs. 101, 102) is delicately attenuate, with a reinforced tip. It is 27μ long and about 5μ wide at the base.

The species was found in the liver of *Lymnaea proxima* in the chara sloughs of the Bitter Root River at Fort Missoula, Montana, in October 1916. It occurred as a minor infection along with *C. dendritica* and *C. gracillima*. The parthenita is an irregular polygonal sporocyst about 0.62 mm. long and 0.38 mm. thick (Figs. 104, 105). At one end is situated a pocket of glandular cells which attach the sporocyst to the host. This is done by the exudation of a mucus. It is doubtful if these cells are at all muscular. At the antipodal end is the germinal epithelium, from which germ balls arise. Only a few cercariae develop within the sporocyst at any one time.

The bladder of the excretory system is truncate, with a common median vessel leading into it from the anterior end. Lining the vesicle at the anterior

end are six gland cells, paired right and left. They appear as small tubercules suspended from the anterior wall of the vesicle. Anterior to the median vessel are two cornua, elongate, yet swollen, reaching antero-laterad around the acetabulum. Near the acetabulum there are received the common posterior and the two anterior tubules. The pattern of the capillaries is racemose. The tail trunk system consists of a common median vessel with many lateral tubules. The entire system is filled with minute excretory granules.

The digestive system consists of a very long esophagus, near the anterior end of which is the small sphincter, and from the posterior end of which the furcae arise. They extend partly around the acetabulum. The salivary-mucin glands consist of right and left paired groups of cells, eight to the group, with long ducts leading in a common bundle to the oral pocket.

In the region of the cerebral ganglion a pair of oval bodies, the non-pigmented eye-spots are located. They are degenerate, similar to those eyes described for *Cercaria gracillima* (p. 52).

The genital cell masses are found in the region of the acetabulum (Figs. 104, 107). To the left is Laurer's canal, and running dextro-laterad is the closely coiled uterus. The genital pore is on the right of the mid-ventral line, anterior to the acetabulum. Running into the ootype from the postero-lateral angles are the vitelline ducts, connecting the vitellaria with the ootype. The testes are not well defined. The relationship of the cercaria is not evident from the genital cell masses.

Cystogenous cell glands are present, altho not as conspicuous as in *C. glandulosa* or *C. micropharynx*. Encystment takes place after a considerable period of free swimming life. Decaudation always precedes encystment. The cyst wall is thin; the animal is easily viewed thru the cyst.

Echinostome Cercariae

Cercaria trisolenata Faust 1917

Cercaria trisolenata represents a unique type of echinostome larva (Fig. 109). It is more attenuate than the average species of this family, and has an unusually short tail. The body has an average length of 0.45 mm. and a width at the preacetabular region of 0.1 mm. The tail is about 0.2 mm. long, lanceolate, and measures 0.06 mm. at the base. An anterior region of the trunk, measuring 0.06 mm. along the median line, constitutes the head region, behind which is a neck-like constriction. There is a collar of 36 spines along the margin of the head, arranged in a single irregular series (Figs. 110, 111). These spines are bluntly rounded at the base and taper to a rounded point at the distal end. They are from 12μ to 14μ in length. The body as a whole is usually covered with minute spines. The acetabulum is beset with an irregular arrangement of crooked spines (Fig. 112). The oral sucker is small but powerful, 33μ in diameter. The acetabulum, situated behind the mid-plane of the body, measures 42μ.

These cercariae, together with *Cercaria gracillima*, are the most cosmopolitan species of the Bitter Root River. They occur in *Physa gyrina* from the

upper and lower reaches of the Valley, and in *Planorbis trivolvis* from the region of Buckhouse Bridge. The infection of the host is always heavy, both as relates to numbers of individuals infected and the number of parasites in the individual host. The per cent of infection ranges from 22 to 100. The parasite is located primarily in the interstices of the liver, but frequently invades the cecal walls and does great injury to the tissues.

The cercaria develops in a redia of well-marked characters (Fig. 117). The redia measures about 1.0 mm. in length and has a mid-diameter of 0.22 mm. and a gross width of 0.35 mm. across the region of the locomotor feet. A small powerful pharynx at the anterior end opens into the rhabdocoel gut which fills the greater part of the body cavity, extending almost to the posterior extremity. The germinal epithelium is at the posterior end. From this layer the ova develop, which grow into cercariae. The first character of the germ ball to become differentiated superficially is the oral sucker (see series of stages in figure 114). Later the tail and the acetabulum become marked off, and finally the oral hood.

At the posterior end a small, non-muscular, truncate bladder is situated. It opens anteriad into two simple unbranched tubes. These can be traced cephalad inside the intestinal ceca to the head of the worm. The cephalic end of the excretory system is unique. Lateral to the pharynx, a triangular channel-system is found. From the anterior angle a small capillary leads forward to a single flame cell. From each of the other two angles a small capillary leads back to a flame cell This constitutes the trisolenate system at the anterior terminus of the excretory tract. The tail excretory tube is a single median structure and has no laterals or terminal outlet. This fact necessitates a revision of the scheme proposed by Cort (1915:37), in which this writer characterizes the excretory system of echinostome cercariae as "opening on each side of the anterior part of the tail." It seems from the present investigation that the three flame cells in the anterior part of the trunk may be a more reasonable criterion for distinguishing the excretory system of this group. Further work on other forms must be done before this can be definitely proposed.

Excretory granules fill the lateral excretory trunks from the pharynx region as far caudad as the acetabulum.

The digestive system is simple. It consists of a long esophagus, with a very small pharynx sphincter about in its middle, and two very long furcae, extending to the sub-caudal region.

The genital cell masses are yet very immature. There are four cell masses present, one on the upper right of the acetabulum (Fig. 130), the vagina; one behind the acetabulum (Fig. 131), the ovary, and two tandem masses in front of the bladder (Fig. 120), the testes. In the vicinity of the ovary are numerous vitelline follicles, but they have not been found to follow any definite pattern.

The nervous system of this species has been made the basis of the discussion on page 49, and needs no further consideration here.

The musculature is almost all parietal, except for the walls of the intestinal tract. Parietal and splanchnic muscles are similar in structure. The former consist of external transverse and internal longitudinal bundles, while the latter consist of external longitudinal and internal transverse fibers (Figs. 118, 119). Each fiber can be traced to a myoblast, the central figure of which is the large oval nucleus, with karyosome and radiating processes, so that the whole figure appears stellate. There are several fibers originating from each myoblast; they always run along a single axis. The longitudinal muscles of the tail are prominent (Fig. 133).

The body is filled with a parenchyma complex, consisting of undifferentiated cells, connective tissue fibers, and cystogenous gland cells. In the tail of an immature cercaria (Fig. 133), there is a partition of parenchyma cells, separating the caudal excretory canals into right and left tubules. This condition disappears as the animal matures, altho vestiges of these cells may be found in the mature cercaria.

The cystogenous cells are differentiated parenchyma cells, filled with a mucoid in the form of oval granules. In the ordinary cystogenous cell (Fig. 113), the granules are about 1μ by 0.6μ in section. There is a central nucleus to each of these cells, with poorly defined membrane separating it from the cytoplasm. It is conspicuous because of its large number of chromatic granules, composed of elongate flecks. These flecks are also present in considerable numbers thruout the cytoplasm; they are especially massed against the cell walls. The glands are best developed in the middle of the body (Fig. 109, sections *bb* and *dd*). Since the cystogenous glands are well developed, the cyst wall is heavy (Fig. 115, A-C). In crawling over the surface of any object the mature cercaria squeezes off the tail by a constriction of the posterior transverse muscles. A final jerk of the tail frees it from the body. Immediately the cystogenous glands pour out a mucus around the contracting worm, so that at first an oval cyst is formed. Later, as it hardens, it assumes a more spherical outline (Fig. 116). Thru this cyst membrane the excretory and digestive systems of the body and the collar spines are readily distinguished. The cysts are so well walled and so numerous that they suggest a considerable period of wintering over.

Cercaria biflexa Faust 1917

Cercaria biflexa belongs to a type of echinostome cercariae distinguished by a smooth body outline, a long powerful tail, blunt oral hood spines and a reflexed excretory tube. The excretory system worked out by Looss (1894: Fig. 191*c*) for *Distomum echinatum* approaches the system in this species to some extent, but differs from it in many details.

The body of *Cercaria biflexa* is elongate ovoid, with a slight constriction just behind the oral hood (Figs. 134, 135). Both the body and the tail are extraordinarily muscular. The body measures 0.45 mm. to 0.5 mm. in length

and 0.13 mm. to 0.15 mm. in width. The tail is at least as long as the body or slightly longer. Its width is about 0.05 mm. at the base. The oral sucker has a diameter of 55μ and the ventral sucker, situated at the beginning of the posterior third of the body, measures 65μ in diameter. Around the oral hood is a circlet of collar spines, 42 in number, ovoid elongate, bluntly rounded at both ends, with a length of 10μ to 15μ and a thickness of 3μ.

The worm was found in *Physa gyrina* in November 1916, and in *Planorbis trivolvis* in May 1917, in the neighborhood of Buckhouse Bridge, near Fort Missoula, Montana.

The parthenita is a redia with a length measurement of 0.4 mm. and a thickness of 0.088 mm. (Fig. 137). The locomotor feet are short, blunt processes in the posterior third of the body, and have a gross span of 0.1 mm. In contrast to the large gut-pouch of *Cercaria trisolenata* parthenitae, the rediae of this species have short inconspicuous rhabdocoel guts, only 0.1 mm. in length. One-third of this is occupied by the pharynx. The body wall is covered with a thick integument, within which is a heavy muscular layer. At the posterior end are a number of small spinous projections (Fig. 141). The germinal epithelium also is at the posterior end. A noticeable feature of the cleaving ova is their flattened condition (Fig. 141). Stages in maturation and cleavage are seen in this figure and may be compared with similar stages of maturation and development in *C. trisolenata* (Fig. 140.) The cercariae, when mature, escape thru the birth-pore situated ventrolaterad.

A prominent excretory system is found in this cercaria (Fig. 135). The vesicle is a cylindrical organ inflated posteriorly. It is not muscular to any marked degree. Tubular cornua empty into the anterior end of the bladder. As these cornua are traced forward lateral tributaries are found to empty into them at regular intervals. In the region of the pharynx the tubes become attenuated and bend twice upon themselves (Fig. 138). The detailed description of this anterior end of the system of *Cercaria biflexa* is found in the section on morphology (p. 40). It may be noted here that there are three flame cells along the course of the ultimate tubule of the system, and that these seem comparable to the three flame cells found in *C. trisolenata*. The excretory tube in the tail is a single median tube for about two-fifths of the way distad, at which point it forks and continues double the remainder of the way distad, with numerous cross-anastomoses. It does not open to the outside either on the sides or end.

The digestive system consists of an extremely long esophagus, extending all the way to the acetabulum; furcae which end at the caudal end of the animal; and salivary-mucin glands, developed to a very high degree. These latter consist of an inner and an outer series of right and left groups (Fig. 134). There are from fifty to sixty cells in each group, in oblong clusters, with a common duct anterior to each series leading cephalad. The two ducts of each side fuse to form a single lateral duct which leads into the oral pocket. These glands are different from the majority of mucin glands in being differentiated

into inner and outer series. The condition is similar in part to that in *Cercaria crenata* (Fig. 55), in which species there is also a double series of glands on each side of the esophagus. But in this case the glands of the inner and outer series are not different in structure and function as in *C. crenata*. Here, too, the ducts are not composed of a bundle of separate ducts, as is found in *C. marcianae* (La Rue, 1917:5), but consist of a single common duct for the entire group of gland cells.

The genital system is much further developed in this species than in *C. trisolenata* (Fig. 139). Behind the acetabulum is the ovary, from which a uterus leads around the acetabulum, ending in a swollen vagina in the pre-acetabular region. Only the transverse ducts of the vitelline system are differentiated. Behind these are the two testes, unequal in size, one above the other.

The encystment of *Cercaria biflexa* is similar to that of *C. trisolenata* in that it depends on the secretion of mucoids from a large number of cystogenous glands in the parenchyma. It differs, however, in the two species both as to time and place of encystment. *Cercaria trisolenata* encysts only after it has escaped from the liver tissues of the host. *C. biflexa* encysts within the host, immediately upon breaking thru the birth-pore of the redia. Thus a section of *Planorbis trivolvis* liver tissue shows the interstices of the liver ceca filled with encysted cercariae, which continue to grow and differentiate within the primary host (Fig. 159).

Furcocercariae

Cercaria gracillima Faust 1917

Cercaria gracillima is a furcocercous cercaria more slender than those previously described. This species, together with *C. tuberistoma* (p. 82), constitute the second instance of furcocercous cercariae to be described for North America, the first being *C. douthitti* Cort (1915:50-52; Figs. 55-64). In addition to the forked-tail character of these three species, they lack a pharynx, and have paired salivary-mucin glands leading into the oral pocket, composed of four or more cells to each group. The "eyelet" excretory anastomosis, connecting the excretory system of the body and the tail is also a common character.

Cercaria gracillima has an oblong cylindrical body (Fig. 142). The branched portion of the tail is elongate lanceolate. The body length varies from 0.13 mm. to 0.16 mm. and the diameter of the worm varies from 0.02 mm. to 0.03 mm. The unbranched portion of the tail is about 0.16 mm. long and the caudal rami are of equal length. The former is 0.02 mm. to 0.03 mm. in diameter and the ramus has a width of 0.01 mm. The trunk is characterized further by the absence of a true oral disc, while in its place there is an invertible sucker. A ventral sucker, 12μ in diameter, varies in location, according to the movements of the animal, from the middle of the ventral side to a position considerably farther forward. The cephalic region is ovately rounded when the sucker is fully distended and is crowned by a cap of small spines. A

feature of this cercaria, in common with that of *C. douthitti*, is the possession of eye-spots (Figs. 144, 150). But the eye-spots of *C. gracillima* are the more vestigial, for they have no pigment.

This species was found in the livers of *Physa gyrina* Say, collected from the lower reaches of the Bitter Root River near Maclay Bridge, Buckhouse Bridge, and the sloughs at the Roadhouse, near Fort Missoula, in the fall of 1916. In addition it was found in the livers of *Lymnaea proxima* Lea from Rattlesnake Creek, Missoula. The infection in most cases was not exceedingly heavy, except in the collection from the sloughs at the Roadhouse, where thirty-three out of seventy-one individuals were infected, or 46.5 per cent.

The cercariae develop in long cylindrical sporocysts, varying in length from 0.25 mm. to 0.1 mm., but most frequently averaging about 0.5 mm. (Figs. 146, 147). In diameter the sporocysts vary from 0.2 mm. to 0.4 mm. The parthenita is a simple structure, non-muscular, depending on the daughter cercariae for its movement. At one end (Fig. 147) is a non-muscular attachment area; at the other end, merely a rounded non-differentiated cap. The germinal epithelium is localized at the attachment end. From this mass the daughter worms develop. Internal pressure from the developing larvae increases the length and diameter of the parthenita. In development (Fig. 148), the ovoid germ ball first differentiates a tail portion; later the rami appear. It is not until considerably later that the acetabulum is found. The oral spines appear only when the larva is mature.

The movement of the cercaria is characteristic for furcocercariae. The main movement consists in a very strenuous beating and lashing of the rami, so that the head is pushed into the object with which it comes in contact. In case the head is not forced into the object, the worm is set free by a backward movement of the tail and the entire worm squirms around until it comes in contact with another object, when the same boring movement is again attempted. The oral end of the cercaria is much better adapted to this type of invasion of the tissues to be infected than if it possessed an oral disc.

The excretory system of *C. gracillima* is embryologically a single paired system for both body and tail. As development and differentiation of parts progress the tubes in the posterior extremity of the trunk and the anterior region of the tail fuse, to form a median bladder and the common tube of the proximal region of the tail. There remains the bifurcated portion in the laterals of the trunk and the rami of the tail, and in addition, the "eyelet anastomosis." This eyelet structure has been observed by Looss (1896:172-174; Pl. 15), in *Cercaria vivax* Sons, and by Cort (1915, Fig. 57) in *C. douthitti*.

The excretory system in the body consists of two lateral tubes that diverge from the bladder and can be traced forward, together with dendritic tubules and capillaries, the internal ones of which frequently form chiasmic anastomoses across the median plane of the body. Slightly posterior to the middle of the body the lateral tube expands and opens into a pocket provided with

cilia (Fig. 145). These cilia come from a flame cell bordering on the lumen of the lateral tube. A second pocket somewhat anterior is an atrium into which many of the capillaries empty; it is filled with small excretory granules, in this way acting as a secondary reservoir.

The digestive system of *C. gracillima* consists of an unbranched esophagus without a pharynx sphincter, a pair of short degenerate furcae extending posteriad beyond the acetabulum, and a ring of gland cells in the region of the esophagus where the pharynx might be expected. Opening into the oral atrium thru common bundles of ducts are the salivary-mucin glands (Fig. 144). These glands are very large with vesicular nuclei. They are situated in the posterior third of the body. In cross section the ducts are similar to those described by Cort (1915, Figs. 59-62) for *C. douthitti.*

The nervous system has been discussed on page 54.

The genital cell masses in the cercaria are hermaphroditic (Fig. 149). Anterior to the acetabulum are the vagina and the cirrus pouch buds, and lateral, extending both anteriad and posteriad, are the vitelline follicles. In the posterior extremity is a conical germinal mass, from which are proliferated anteriad a number of small testicular follicles.

The general features of this fluke make it possible to refer it to the Schistosomatidae.

Cercaria tuberistoma Faust 1917

This species of cercaria is shorter and much more muscular than *C. gracillima.* The body is elongate ovoid, with the anterior end slightly constricted and crowned with a pair of tuberosities (Fig. 155). The body length is about 0.2 mm. and the width 0.05 mm. to 0.06 mm. The tail measures about 0.32 mm. as a whole, equally divided into common portion and rami. There is no oral suctorial disc, but instead the oral invertible proboscis. The acetabulum measures 0.03 mm. in diameter.

The cercaria was secured from a single light infection of *Physa gyrina* collected in the Bitter Root River at Corvallis, Montana, in October 1916. Out of nineteen snails examined only one was infected. Only a few cercariae were secured, and these were studied as live mounts. From this study the excretory, digestive and general body features were worked out.

The cercaria develops in an elongate, dumb-bell-shaped sporocyst, spreading out at one end to form an attachment disc (Figs. 157, 158). At the end opposite the attachment organ the cercariae develop from the maturation of the germinal epithelium. They escape thru a rent in the wall of the sporocyst. Stages in development (Fig. 158, A-E) are similar to those described for *C. gracillima* (Fig. 143). On the whole the embryos of this species are stouter than those of *C. gracillima.*

The excretory system has the features common to all furcocercariae. The bladder and the eyelet are muscular (Fig. 155). The lateral tubes are of small diameter, with anterior and posterior tubules. No anastomoses take

place in the cercariae of this species. The median tail tube receives six lateral tributaries, the anteriormost of which is reflexed. The rami have each an unbranched tubule.

The cephalic region is marked by a large invertible sucker, extending thru the anterior third of the body. No intestinal ceca whatever have been observed in this species. No glands surround the esophagus as a distinct ring, altho the entire esophageal tube lining is glandular in nature. Four small salivary-mucin glands are situated in the posterior third of the body (Fig. 155). Their thick ducts empty into the oral cavity as heavy bundles. The cells of this system are filled with closely aggregated, deeply staining granules. The nucleus of the salivary-mucin gland cell is extremely small.

This species possesses neither pigment eye nor eye-spot without pigment.

Encystment has not been observed in this species.

Cercaria tuberistoma is probably a schistosomatid larva.

PATHOLOGY

The infection in any case of internal parasitism suggests an inquiry as to the effects of the parasite on the host. The injury on the human subject produced by trematode infections has been the subject of numerous observations and records. Notable among these are the contributions of Looss (1913) on *Schistosoma haematobium*, Katsurada (1914) on *Schistosoma japonicum*, and Ward (1909) on *Fasciolopsis* spp. Again, the effect of trematodes on their host has been the subject of considerable study in fish infection, on account of the economic importance of the problem. But where the special incentives to the problem have been lacking, very little study has been made on the pathological significance of trematode infection.

The helminth parasite causes a two-fold injury to the host, mechanical and chemical. The inclusion of parasites within the organs of the host is the occasion for distension of the organs and consequent irritation; the piercing of organs of the host by the armature of the worm, an actual mechanical injury. These injuries are accompanied by the formation of fibromata within the organs and, usually, attempts to isolate the parasite by the secretion of a cyst around it, as in schistosomiasis (Bovaird and Cecil, 1914:191). In the ordinary infection a toxin is secreted by the parasite, and frequently an antithrombin and a hemolysin are produced. Such injuries as these in higher animals are diagnosed by the blood-picture, where excessive hemocytolysis and eosinophilia are found.

The infected organs of the molluscan hosts of the Bitter Root Valley are the liver ceca. Altho these lie next to the testes, the worms have never been found to invade these organs. Thomas (1883:114) found that the cercariae of *Fasciola hepatica* live normally in the pulmonary chamber of the snail *Lymnaea trunculata*. Cort (1915) found the infected organs of the Campelomas were the gills, but in other species, the liver tissues were the seat of the infection. The infected tissue of the Venezuelan snail, *Planorbis guadelupensis*, is the testicle according to observations made by the writer.

The liver ceca consist of polygonal lymphocytoidal cells grouped around the lumina of the ceca, with an epithelial lining surrounding the ceca. Among the ceca are large interstices filled with lymph. These intercecal spaces are the places where the worms are first found, suggesting invasion thru the blood stream. In light infections, the parthenitae lie here, absorbing the nourishment from the surrounding liquid in which the worm is bathed. The only mechanical injury up to the time of the activity of the cercariae is caused by the agitation of the developing larvae encysted within the host. But in the case of heavy infection, especially where the larva does not encyst within the host, where it works its way out into the water, even a few worms may cause considerable mechanical harm to the host.

In an examination of living material and sections of infected mollusk liver tissue, no infection was found to be so light that the host was unharmed. In

the *Cercaria biflexa* infection of *Physa gyrina* (Fig. 159), where the cyst membrane is moderately heavy, many ceca are uninjured, yet some betray the marks of injury. One such injury is shown in the figure. In this case the cells of the ceca have undergone only a little change. A comparison of this condition with that of *C. micropharynx* infection in *Lymnaea proxima* (Fig. 160) and *C. gracillima* infection in *Physa gyrina* (Fig. 161), shows a comparatively small injury in the former tissue and a severe injury in the latter tissues. Both the latter cases show tissue degeneration. The chemical change in *Lymnaea proxima* is evinced by 1) fatty bodies that have accumulated in some of the cells (*a*), showing as highly refractive inter-cellular inclusions; 2) large vacuoles in the cells (*b*), especially around the nuclei; 3) cytolysis and karyolysis (*c, d*), including a sloughing of the tissues in the region of the lumina of the ceca. The condition of *C. gracillima* infection in *Physa gyrina* (Fig. 161) pictures a further degeneration of the tissues. Fatty globules (*b*), are common, usually accumulated as spherules within the wall. Vacuolization (*d*) has progressed to an advanced stage. Cytolysis and karyolysis (*a, c*) have gone so far that the outlines of the majority of the cells are indistinct and no difference exists longer between the epithelial and the lymphocytoidal cells. An indefinite, irregular margin marks off the ceca from the interstices in which the cercariae lie. A further change consists in the formation of fibromata (*e*) and granulomata within the degenerating ceca. Finally the epithelium surrounding the entire liver mass has been penetrated by sand granules (*f*), and other foreign bodies have had access to the tissues.

In the infection of *Planorbis trivolvis* with *C. trisolenata* the mass of the worms was about twice that of the liver tissue infected. The tissue was so distended with the parasites that a prick of the needle was sufficient to cause the liver membrane to burst, upon which the rediae and cercariae fairly poured out of the tissue.

The data on the effect of the trematode infection on the molluscan host are significant. No infection is so light that mechanical and chemical injuries are not inflicted. In the heavy infections such as are common to the mollusks of the Bitter Root Valley, the injury is so heavy that it must alter appreciably the life of the host. The mechanical pressure tends to inhibit or increase the functioning of the glandular organs and cramps the tissues within unusual confines. The presence of foreign proteins in close association with the lymph sinuses is sufficient to alter the vital economy of the host. The boring of the worm destroys the tissues locally and in general irritates the mechanism, exposing it to bacterial infection. The secretion of digestive juices by the parasite, and of anti-thrombins and possibly specific poisons, upsets the entire physiological equilibrium of the organism.

PROBLEMS PRESENTED

INTERRELATION OF TREMATODES

In working out new species of organisms, especially from new geographical areas, there are often physiological and morphological facts that are of general significance in the light of previous studies. Relationship is the ultimate problem for all workers in morphology. While light is shed on phylogeny by the discovery of new species, it is futile to expect to found a system of phylogeny on a single species. With these limitations in mind the writer presents some of the more important questions that arise from the study of the trematodes of the mollusks of the Bitter Root Valley.

In the early days cercariae and rediae were considered as different groups of the animal kingdom, and it was not until the life-history studies of Leuckart, La Valette (1855), and Ercolani (1881, 1882) had been published that the genetic relationships of cercariae and parthenitae were established. The germ layers of all generations of trematodes have a similar origin, and important structures of the group present the same problem.

Certain investigators of recent time have come to regard the trematodes as a polyphyletic group. Their conclusion has resulted, perhaps, from their lack of study and consequent inability to recognize the fundamental resemblance of the genital, excretory and nervous systems of the various sub-divisions of the group, especially during the developmental stages.

From more convincing observations Odhner (1907) has concluded that the Monostomata are polyphyletic. He has noted among certain monostomes a structure comparable to the pharyngeal pockets of amphistomes, and among others a primitive acetabulum (1911). In a study of monostome cercariae from the Bitter Root Valley, the similarity of the nervous system and genital cell masses of *Cercaria pellucida* and of those systems in *Gastrothylax gregarius* Looss has been investigated.

Both *Cercaria pellucida* and *Gastrothylax gregarius* show paired brain ganglia closely set together with only slight constriction of the dorsal commissure. In both species the nerve cells lie superficially upon the central nerve ganglion masses. Moreover, relatively large posterior ventral and smaller lateral and dorsal trunks, together with their respective positions, constitute a series of similarities not to be overlooked. The lack of pharyngealis, palatinus, and dorsolateral commissure (Figs. 123, 124) serves to show that the nerve complex of the monostome larva *Cercaria pellucida* is not typically distomate. Its nerve structures are much more readily referred to the Gastrothylax type.

In the second place certain features of the genitalia of *Cercaria pellucida* and Gastrothylax suggest a common ancestry. The median ovary in the subcaudal region; the paired testes lateral to the ovary; the dendritic vitellaria, located in two series, and, finally, the parallel course of the uterus and

the vas efferens to the genital pore far cephalad—all of these show in common a genital system quite distinct from the usual distome types.

The similarity of the nervous and genital complexes of larval monostomes, such as *Cercaria pellucida* and *C. konadensis*, and the amphistome, *Gastrothylax gregarius*, suggest a common origin of certain monostomes and amphistomes.

Among adult distomes there is great variety of structure, yet only in one family, the Schistosomatidae, has the nervous system been fundamentally altered. The structures of the two furcocercous larvae, *Cercaria gracillima* and *C. tuberistoma*, demonstrate their relationship to the Schistosomatidae. The reasons for this belief are these:

The characters which distinguish the apharyngeal furcocercous cercariae are as follows: 1) a forked tail (larval character only); 2) paired groups of salivary-mucin glands (larval); 3) absence of an oral suctorial disc, and in its place 4) an invertible suctorial proboscis; 5) an apharyngeal esophagus, provided with glands in the region usually occupied by a pharynx. The nervous system, more deeply seated, is modified by the degeneration of the posterior laterales during early embryonic development, and the fusion of the posterior dorsales with the posterior ventrales about one-third the body length back from the anterior end (Fig. 150). All of these, except the forked tail and the salivary-mucin glands, are both larval and adult characters. In addition, the larva of *Cercaria gracillima* has several testicular follicles proliferated from the testes-mass at the posterior end of the body.

Certain of the structures of this group also characterize the larvae of other groups of trematodes. For example, *Cercaria cristata* La Val. (1855:23; Taf. II, Fig. K), has a bifid tail and apparently lacks a pharynx, but the fact that it lacks an acetabulum probably separates it from the distome furcocercariae. Among the Gorgorderinae there are apharyngeal cercariae with several testes. However, Ssinitzin (1905:46-51; Taf. I, II) has shown for four Gorgordera species, that the cercariae are characterized in common by 1) a stylet, 2) salivary glands only in the cephalic region of the body, 3) a large glandular excretory vesicle, almost filling the posterior third of the body, and 4) a disproportionately large tail, showing the cystocercous relation of the larvae of the group. Moreover, the nervous system of the Gorgorderinae is typically distomate (Zailer 1914:386).

It may be stated with considerable probability that all of the fundamental organs of the furcocercariae, namely, the apharyngeal esophagus, the multiple testes, and the uniquely modified nervous system, are found in only one family, the Schistosomatidae. All described Schistosomatidae are characterized by the absence of a true oral suctorial disc and by the presence of an invertible oral suctorial pouch. They have no pharynx, but in its stead glands that line the wall of the esophagus. Looss has described the modified nervous system of the family in his study of *Schistosoma haematobium* (1895:

60-68; Taf. II, Fig. 18). It corresponds in detail to the system in *Cercaria gracillima* previously described.

Coupled with these morphological likenesses are the experimental data of Leiper (1915, 1916), Miyuri and Suzuki (1914), and Iturbe and Gonzalez (1917) on Schistosoma life-histories. Leiper has found that the three schistosome species known to infect man, *Schistosoma haematobium*, *S. mansoni*, and *S. japonicum*, give rise to miracidia which have a certain attraction for certain snails in the districts infected. Within the tissues of these snails the miracidia metamorphose into sporocysts, and the second generation sporocysts give rise internally to bifid cercariae with a ventral sucker but without a true pharynx. Furthermore, these cercariae introduced thru the skin of experimental animals, mice and monkeys, give rise to typical unisexual adult schistosomes.

This two-fold evidence favors the view that the furcocercous apharyngeal distome cercariae, including *Cercaria gracillima* and *C. tuberistoma* of the Bitter Root fauna, develop, under proper conditions, into adult schistosomes. One character figured by Leiper for all of his apharyngeal bifid cercariae, yet not used by him as a diagnostic character, is the presence of salivary-mucin glands. On the other hand, one character used by Leiper for cercariae of the group, namely, the absence of a pigment eye, holds for his three species of schistosome larvae, but does not hold for *Cercaria ocellata* La Val., *C. douthitti* Cort, or *C. gracillima*. It has been shown that the eye-spot may be present without pigment (*C. gracillima*). Likewise the failure of Looss to mention an eye-spot for *C. vivax* Sons. (1896:216-223; Figs. 172-174) does not necessarily imply the absence of pigmentless eye-spots in that species.

The relationship of the forked tail apharyngeal distome cercariae will be made much clearer by a consideration of the genital organs. The adult Schistosomas into which the larvae of Leiper develop are characterized by a relatively small number of testicular follicles, 4 to 5 for *S. haematobium*, 6 to 8 for *S. japonicum*, and 8 for *S. mansoni*. On the other hand, the testicle proliferation in *Cercaria gracillima* (Fig. 149) shows twenty-four or twenty-five follicles already differentiated from a posterior germ mass. The large number of testicular follicles has been found to be characteristic of the adult Schistosomatidae of the genera Bilharziella (Kowalewski,1895; 1896), Gigantobilharzia (Odhner, 1912), and Ornithobilharzia (Odhner, 1912). None of these genera and in fact no Schistosomatidae have been reported from North America.

From these considerations it seems probable that *Cercaria gracillima* is the larva of a schistosome genus, such as Bilharziella, Ornithobilharzia or Gigantobilharzia, all of which are bird parasites.

Since the germinal masses of *Cercaria gracillima* are hermaphroditic, and any marked differentiation of the organs does not take place while the larva is outside the definitive host, differentiation of sex in Schistosomatidae takes place in these species comparatively late in their metamorphosis. This view

is in keeping with the studies of Odhner (1912), who points out the fundamental morphological relationship of the hermaphroditic species Liolope and Haplometra to the unisexual Bilharziella, Gigantobilharzia, Ornithobilharzia, and Schistosoma.

The discussion leads to the conclusion that the furcocercous larvae possess in common 1) a bifid tail, 2) a ventral sucker, 3) an oral suctorial pouch which can be inverted, 4) a glandular esophagus without sphincter muscles, 5) paired groups of salivary-mucin glands, four or more to the group, 6) multiple testes, and 7) a specifically modified nervous system. In the light of present knowledge all of these species fall within the limits of the family Schistosomatidae.

Of all the known groups of trematodes the Holostomata have been the group of least genetic study and most erroneous interpretation. On account of their large size the adult holostomes have been known for many years and dozens of species have been described. Nothing, however, has been known of the parthenitae and their development. Without sufficient evidence Brandes (1891:573) has interpreted the sketch of a miracidium of *Strigea* (*Holostomum*) *cornucopiae* Molin (von Linstow,1877, Fig.30) as a metamorphosing tetracotyle. In other words, Brandes concludes that the holostome has a direct development without the intercalation of a parthenogenetic cycle. Ercolani (1881:284-290; Tav. II, Figs. 16-22) has worked out the life-history of *Strigea erratica* (Duj.) from the tetracotyle to the adult form, by infecting *Anas* sp. with *Tetracotyle typica* cysts from the mollusk *Planorbis corneus*. Altho Ercolani found a tetracotyle in a sporocyst (Tav. II, Fig. 18), he interpreted it as the invasion of the tetracotyle into the sporocyst of *Cercaria ocellata* La Val. Ssinitzin (1910:22, 23) has justly criticized Brandes' conclusion of the monogenetic development of holostomes, but in lieu of true holostome evidence in support of the digenetic view he has substituted evidence from *Cercaria plicata*, a peculiar distome larva which he has found to bear certain relationships to the holostomes.

It has been shown in this paper (p. 16) that there are parthenogenetic cycles in *Cercaria flabelliformis*, a typical holostome, and that several generations of rediae are intercalated between the miracidium and the tetracotyle. Thus, there is conclusive proof that the holostome has an alternation of generations, hermaphroditic and parthenogenetic, similar in kind to such alternation in other Digenea.

In spite of the strangely modified suctorial apparatus and posterior genital organs of the holostomes, there seem to be good grounds for believing that they originated from the distomes. They have an acetabulum, and frequently the muscular rudiment of a genital pore just in front of the acetabulum (Fig. 52). On the other hand it is very doubtful if the lappets (Zapfenlappen of Brandes 1892, Taf. 41, Figs. 5-15) bear any homology to the genital pore rudiment. It has been shown, in fact, that the lateral lappets in *Cercaria flabelliformis* arise from a pair of oval suctorial grooves (Fig. 41), and that in

Tetracotyle pipientis (Fig. 47), where these grooves remain rudimentary, no lateral lappets develop.

As von Linstow (1877:189) pointed out, species characters in Strigea (Holostomum) have been treated very superficially, since the group members are not readily distinguished by external markings and the internal anatomy is difficult to interpret. Yet the writer has found that even in the early larva the points of differentiation are well marked. The parthenogenetic egg of the holostome developing into the cercaria is at the time of maturation structurally different from the ova developing into a redia. Thus the actual phylogenetic history of the group is hidden by its precocity and the developmental stages of the holostome show only in telescopic fashion the actual ancestral history.

Extraordinary nerve modification in the holostomes (Fig. 53) is related directly to the modification of the muscle complex. This modification consists usually in the degeneration of the posterior dorsales and laterales, and a relative increase in size and importance of the posterior ventrales. The other systems of the holostomes, especially the genital and excretory organs, are equally highly modified and equally well formed in the larva. Ssinitzin (1910, 1911) has suggested that the change in the genital pore from the preacetabular position to the posterior ventral extremity has come about thru the formation of a new opening rather than thru a shifting of the old preacetabular pore. The original pore is still present in the larvae, altho in most cases there is no clue to its former connection or function. The extent of these changes indicates a long period of gradual adjustment to a modifying environment.

The study of the cercariae of the various groups of the Digenea not only serves to supplement relationship studies in adult hermaphroditic generations of trematodes, but also brings out structural relationships very considerably if not entirely hidden in the adult. The most constant of all the systems in the group Digenea is the nervous system. Any marked modification from the characteristic distomate type is indicative of a considerable period of divergent growth.

The fundamental systems of the hermaphroditic generation of the trematode are deep seated; they are well formed in the cercaria, and little significant differentiation takes place during metamorphosis.

RELATION OF TREMATODES TO OTHER GROUPS

Among the early systematists Trematoda were classified with the Hirudinea because of the common superficial resemblance of the two groups. Even as late as 1871 Schmarda separated the Trematoda from the Turbellaria and Cestoda, and placed them with the Hirudinea in the Cotylidea. Balfour (1881:316, 317) considered a direct relationship of all Metazoa above Coelenterata entirely unsatisfactory and conceived the idea of referring them all back to the trochophore larva which possessed radial symmetry. In his

monograph on *Amphistomum subclavatum*, Looss (1892:156, 157) compared the proliferation of the germ-balls from the body wall of the parthenita to the production of eggs and spermatozoa in the marine polychaetes, and suggested that other embryonic structures of the trematode were comparable to annelid structures, so that they might be considered of phylogenetic value. Recently Ssinitzin (1911:86) has spoken of the resemblance of the Trematoda to Arthropoda and Trochelminthes, in view of the absence of any ciliary integument, in place of which, he says, the cuticula and the external skeleton develop.

During this time the theory of the common descent of the Trematoda, Cestoda and Turbellaria has been gaining ground, not because they are all "flatworms," as Ssinitzin insists, but on the homologies of the genital, excretory and nervous systems. The observations of Leuckart (1886:140), Schulze (1853:178-195), and Schneider (1864:590-597) all support this view, while Leuckart even saw the analogy between the gutless sporocyst and the Acoela. Lang (1884:669) showed that the nervous system of the Trematoda and Turbellaria was homologous.

With the work of Haswell on Temnocephala (1888) the close affinities of the Trematoda and the Turbellaria became evident. In this group the excretory system, the three anterior and posterior nerve trunks, the anterior mouth, and the dorsal pigment eyes—all these bridged the way for the acceptance of the thesis that the Trematoda and the Turbellaria have a common ancestry.

The study of the parthenogenetic generations of the Digenea, to which this paper is devoted, stands in support of this thesis and contributes the following facts towards its further acceptance.

1. The body cavity of the hermaphroditic generations of trematodes and of Turbellaria is filled with differentiated mesenchyme and connective tissue. In the parthenitae the parenchyma is confined to the body wall because it is less differentiated.

2. Both Trematoda and Turbellaria are typically flat, with a pronounced bilateral symmetry. The cylindrical appearance of the parthenitae is a secondary modification due to parasitism.

3. The epidermis of Trematoda and Turbellaria consists of a single layer of cells. In the sporocyst larva, the miracidium, and in the Turbellaria, the epithelial layer is ciliated. In the rediae and in the cercariae the layer is usually sloughed off before maturity and in its place the basement membrane of mesodermal origin, serves as the integument.

4. The nervous system of the Monogenea, the Digenea, and the Turbellaria is reducible to a common type. Two brain ganglia with a transverse commissure, three anterior pairs of nerve trunks, and three anterior pairs of nerve trunks—these are common to all three groups. Moreover, the pigment eyespots of the Turbellaria, Monogenea, and Digenea are not only homologous, but practically identical in detail (Hesse 1897; and page 52 this paper). In

each case one or more ganglion cells fill the optic cup. In each it can be traced to the brain center. Parasitism has caused the pigment eye to degenerate in most adult Digenea. Even in the cercariae it is pigmented only in certain species; other species have lost all traces of pigment, but the optic nerve is still present and can be traced to the brain center. In many cases it has been lost, even in the cercariae. Eye-spots are common in miracidia, but are lost on metamorphosis into the sporocyst. There are no records of eyes in rediae.

5. The digestive tract of the cercariae and the adult hermaphroditic generations of trematodes is usually triclad. In the redia the gut is rhabdocoel; there is a pharynx and salivary glands have been described (Ssinitzin, 1911, and pp. 63, this paper). In the miracidium, there is an indication of a rhabdocoel gut and salivary glands (Looss, 1892; Miyuri and Suzuki, 1914), altho these are usually lost in the adult. In the Turbellaria the gut is triclad, polyclad, rhabdocoel or acoel. The pharynx is ordinarily present and salivary glands are common.

6. The excretory system in the two groups is at first a single pair of protonephridia. This condition is found in miracidia, rediae, cercariae and Turbellaria alike. The capillaries, whether in the larva or adult, end in flame cells.

7. The genital system was one of the first in which investigators recognized the relationship between the Trematoda and the Turbellaria. The hermaphroditic condition in the hermaphroditic generation of the Trematoda is strikingly similar to that of the Turbellaria, with the common genital atrium in all groups except Acoela. Parthenogenesis in parthenitae is the result of the great change in environment of these cycles.

Thus the main trend of investigation has come to support the common origin of the Trematoda and the Turbellaria.

LIFE CYCLE OF THE DIGENETIC TREMATODES

The life-history of the trematode of the order Digenea consists not in an alternation of sexual and asexual generations, but rather of successive sexual generations which are parthenogenetic and hermaphroditic.

A problem which has arisen in connection with the genitalia of the Digenea is the significance of Laurer's canal. Looss (1893a) considers it homologous to the uterus of Cestoda, while Goto (1893) believes it to be the homolog of the blind vagina of Amphilina and the genito-intestinal canal of Monogenea. According to Lühe (1909) a Laurer's canal is present in Monostomes, and in some groups of the distomes, including Plagiorchiidae and Echinostomidae. It has not been recorded for holostomes or Schistosomatidae. Except for the Echinostomid cercariae, a Laurer's canal has been found in all cercariae of the groups studied by the writer, where the adult trematode has the canal. Absence of the canal in Echinostomid cercariae can be explained on the basis of late development of the genital organs in this family. On the other

hand, no Laurer's canal has been found in the groups where no canal is present in the adult. Students of cercariae have not as a rule recorded the canal in trematode larvae. Ssinitzin (1905, Figs. 62, 67, 74) has found it in the three xiphidiocercariae, *Cercaria gibba* de Fil., *C. prima*, and *C. secunda*. The constant development of this organ in the several groups described in this paper shows that the canal originally had an important place in the genital processes of the Digenea.

The pronounced difference in structure between parthenogenetic ova which develop into rediae and those which develop into cercariae has been discussed (p. 18). This difference has been found to bear no relation to the phenomenon of maturation, since the chromosome count in the mature cells is the same, whether redia or cercaria is to be produced. In fact, it seems probable that the differentiation occurs before maturation. It is significant that the ova which develop into redia are comparatively simple while the ova which develop into cercariae are extremely complex. In this connection it has been observed that embryos developing from germ-balls produced from ova free in the body cavity produce daughter rediae. The maturing ova from the germinal epithelium lodged in the body wall of the parthenita develop either into rediae or cercariae.

In his experiments on planarians Child (1915) has shown that starvation and fragmentation (fission) secure a rejuvenescence for the individual. The less differentiated individual is on the whole the younger one. From the present study on the life-history of trematodes there is justification for the belief that the undifferentiated eggs produce daughter parthenitae because they are simple, i.e., younger, while the more highly differentiated eggs grow into cercariae because they are physiologically old. Interpreted in this light, the parthenitic individuals of the Digenea are physiologically younger than the cercariae and the adult hermaphroditic forms because their structure is simpler. They have sacrificed complexity of structure to meet the needs of the parasitic life, and in so doing have become remarkably rejuvenated. In two species, *Cercaria diaphana* and *C. micropharynx* extreme simplicity has been assumed in the sporocyst, for the germ-balls develop from any cell of the body wall.

The writer believes that the ability of the parthenita to reproduce daughter rediae or sporocysts for two or more generations rests on the simplicity of the ovum and the relative simplicity of the parthenita, especially as regards the undifferentiated mesoderm cells. If this rejuvenation can be continued indefinitely, the parthenogenetic generations can also continue indefinitely without the intercalation of the hermaphroditic cycle.

Child (1915:407) has stated that "in many cases parthenogenetic eggs are apparently less highly differentiated morphologically, and younger physiologically, than zygogenic eggs of the same species." The present study makes it necessary to add that in cases where the parthenogenetic eggs may develop into parthenitae or cercariae, the eggs which develop into the former

individuals are apparently less highly differentiated morphologically and younger physiologically than those which develop into cercariae.

Finally the present study causes the writer to support the view that the hermaphroditic phase of the life cycle of the Digenea is more closely related to the ancestral group than the parthenita, and that the simplicity of the parthenita has been assumed secondarily. This conclusion is based on the evidence that the original type was a highly complex Platyhelminth with ciliary integument and eye-spots, characters found only in the miracidium. The modification of the parthenita has come about as the direct result of parasitism. It has lost its mesenchymatous matrix, its excretory tract has been extraordinarily modified, and its germ cells have become uniquely simple. The nervous system of the redia has been simplified while the sporocyst lacks a nervous system entirely. In the sporocyst even the muscle cells have remained undifferentiated. Thus complexity in the hermaphroditic generation of Digenea is an index of the unmodified condition of the group most early related to the prototype.

SUMMARY

1. Trematode infection of mollusks of the Bitter Root Valley, Montana, is heavy.

2. The history of the germ cells of the sporocyst and redia show them to arise parthenogenetically.

3. Parthenitae and adult hermaphoditic trematodes are comparable individuals: likewise their germ cells can be referred to a common type of germinal epithelium.

4. The integument of trematodes is mesodermal in origin.

5. The fundamental systems of the adult hermaphroditic trematode are well developed in the cercaria.

6. The excretory, genital and nervous systems of the cercaria may be used to show the natural relationships of the larvae.

7. Holostomes, like distomes, monostomes and amphistomes, have an alternation of hermaphroditic and parthenogenetic generations.

8. Holostomes are probably of distome origin.

9. Parthenitae are well adapted to their parasitic life because their structure is simple, in consequence of which they have become physiologically young.

SPECIES DESCRIBED IN THIS PAPER.

MONOSTOMATA
- *Cercaria pellucida* Faust 1917
- *Cercaria konadensis* Faust 1917

HOLOSTOMATA
- *Cercaria flabelliformis* Faust 1917
- *Tetracotyle pipientis* nov. spec.
- *Cercaria ptychocheilus* Faust 1917

DISTOMATA

Xiphidiocercariae
- *Cercaria crenata* Faust 1917
- *Cercaria glandulosa* Faust 1917
- *Cercaria diaphana* Faust 1917
- *Cercaria dendritica* Faust 1917
- *Cercaria micropharynx* Faust 1917
- *Cercaria racemosa* Faust 1917

Echinostome Cercariae
- *Cercaria trisolenata* Faust 1917
- *Cercaria biflexa* Faust 1917

Furcocercariae
- *Cercaria gracillima* Faust 1917
- *Cercaria tuberistoma* Faust 1917

BIBLIOGRAPHY

ANDRÉ, J.
1910. Zur Morphologie des Nervensystems von Polystomum integerrimum Froel. Zeit. wiss. Zool., 95:191-220; 13 textfigs.

BALFOUR, F. M.
1881. A Treatise on Comparative Embryology, vol. II. London, 655 pp.

BARKER, F. D., and LAUGHLIN, J. W.
1911. A New Species of Trematode from the Muskrat, *Fiber zibethicus*. Trans. Amer. Micr. Soc., 30:261-274; 1 pl.

BETTENDORF, H.
1897. Ueber Musculatur und Sinneszellen der Trematoden. Zool. Jahrb., Anat., 10:307-357; 5 Taf.

BLANCHARD, E.
1847. Recherches sur l'organization des vers. Ann. sci. nat., zool. (3) 8:271-341; 5 pl.

BLOCHMANN, T.
1896. Die Epithelfrage bei Cestoden und Trematoden. Sep., 6ten Vers. deutschen Zool. Ges. zu Bonn. Hamburg. 12 pp., 2 Taf.

BOVAIRD, D., and CECIL, R. L.
1914. Schistosomiasis japonica; a Clinical and Pathological Study of Two Cases. Amer. Jour. Med. Sci., 148:187-206; 3 figs.

BRANDES, G.
1891. Die Familie der Holostomiden. Zool. Jahrb., Syst., 5:547-604; 3 Taf.
1892. Zum feineren Bau der Trematoden. Zeit. wiss. Zool., 53:558-577; 1 Taf.

BRAUN, M.
1893. Vermes. Trematodes. Bronn's Thierreich, IV, 1A. Leipzig. pp. 306-925; 27 pl.
1901. Zur Revision der Trematoden der Vögel. I. Centralbl. Bakt. u. Parasit., Orig. (I) 29:560-568.
1901a. Zur Revision der Trematoden der Vögel, II. Centralbl. Bakt. u. Parasit., Orig. (I) 29:895-897, 941-948.

BROWN, A. W.
1899. On *Tetracotyle petromyzontis*, a parasite of the Brain of Ammocetes. Quar. Jour. Micr. Sci., 41:489-498; 1 pl.

CARY, L. R.
1909. The Life History of Diplodiscus temperatus Stafford. With Especial Reference to the Development of the Parthenogenetic Eggs. Zool. Jahrb., Anat., 28:595-659; 4 pl.

CHILD, C. M.
1915. Senescence and Rejuvenescence. Chicago. 481 pp.

COE, W. R.
1896. Notizen über den Bau des Embryos von Distomum hepaticum. Zool. Jahrb. Anat., 9:561-570; 1 Taf.

CORT, W. W.
1914. Larval Trematodes from North American Fresh-Water Snails. Jour. Parasit., 1:64-84; 13 Figs.
1915. Some North American Larval Trematodes. Ill. Biol. Monogr., 1:447-532; 8 pl.

DIETZ, E.
1910. Die Echinostomen der Vögel. Zool. Jahrb., Suppl., 12:265-512; 6 Taf.

ERCOLANI, G.
1881. Dell' adattemento della specie all' ambiente. Nuove ricerche sulla storia genetica dei Trematodi. I. Mem. r. Acc. Ist. Bologna., (4) 2:239-334; 3 Tav.

1882. Dell' adattemento della specie all' ambiente. Nuove ricerche sulla storia genetica dei Trematodi. II. Mem. r. Acc. Ist. Bologna., (4) 3:43-111; 3 Tav.

FANTHAM, H. B.

1916. The Animal Parasites of Man. London. 900 pp. 415 Figs.

FAUST, E. C.

1917. Notes on the Cercariae of the Bitter Root Valley, Montana. Jour. Parasit., 3:105-123; 1 pl.

DE FILIPPI, Ph.

1857. Troisième mémoire pour servir à l'histoire génétique des Trématodes. Mém. Acad. Sci. Turin., (2) 18:1-34; 3 pl.

FISCHER, P. M.

1883. Ueber den Bau von Opisthotrema cochleare nov. genus, nov. spec. Zeit. wiss. Zool., 40:1-42; 1 Taf.

GAFFRON, E.

1884. Zum Nervensystem der Trematoden. Zool. Beitr., 1:109-115; 1 Taf.

LA VALETTE ST. GEORGE.

1855. Symbolae ad Trematodum Evolutionis Historiam. Berolini 40 pp., 2 Taf.

GOTO, S.

1893. Der Laurer'sche Kanal und die Scheide. Centralbl. Bakt. u. Parasit., Orig. (I) 14:797-801; 4 Figs.

1894. Studies on the Ectoparasitic Trematodes of Japan. Jour. Coll. Sci. Imp. Univ. Japan., (1) 8:1-273; 27 pl.

HASWELL, W. A.

1888. On Temnocephala, an Aberrant Monogenetic Trematode. Quart. Jour. Micr. Sci., 28:279-302; 3 pl.

1903. On Two Remarkable Sporocysts Occurring in Mytilus latus on the Coast of New Zealand. Proc. Linn. Soc. N. S. Wales, 27:494-515; 2 pl.

HAUSMANN, L.

1897. Über Trematoden der Süsswasserfische. Rev. suisse zool., 5:1-42; 1 Taf.

HESSE, R.

1897. Untersuchungen über die Organe der Lichtempfindung bei niederen Thieren. II. Die Augen der Platyhelminthen. Zeit. wiss. Zool., 62:527-582; 2 Taf.

HOFMANN, K.

1899. Beiträge zur Kenntnis der Entwicklung von Distomum leptostomum Olsson. Zool Jahrb., Syst., 12:174-204; 2 Taf.

ITURBE, J. and GONZÁLEZ, E.

1917. The intermediate host of *Schistosomum mansoni* in Venezuela. Natl. Acad. Med. Caracas. Sep. 7 pp., 2 pl.

JÄGERSKIÖLD, L. A.

1891. Ueber den Bau des Ogmogaster plicatus (Creplin). Kgl. svenska Vetensk. Akad. Handl., (7) 24:1-32; 2 Taf.

JOHNSTON, S. J.

1904. Contributions to a Knowledge of Australian Entozoa. III. On Some Species of Holostomidae from Australian Birds. Proc. Linn. Soc. N. S. Wales, 29:108-116; 3 pl.

1916. On the Trematodes of Australian Birds. Jour. Proc. R. Soc. N. S. Wales, 50: 187-261; 11 pl.

JUEL, H.

1889. Beiträge zur Anatomie der Trematodengattung Apoblema (Dujard.). Kgl. Sv. vetensk. Akad. Handl., (4) 15:1-46; 1 Taf.

KATSURADA, F.

1914. Schistosomiasis japonica. Centralbl. Bakt. u. Parasit., Orig. (I) 72:383-379; 2 Taf.

KOWALEWSKI, M.
1895. Studya helminthologiczne. III. Bilharzia polonica, n. sp. Rozpraw Wydz., mat.-przyr. Akad. Umiejet. Krakowie, (1) 31:1-30; 2 pl.
1896. Studya helminthologiczne. IV. Bilharzia polonica, n. sp. Rozpraw Wydz., mat.-przyr. Akad. Umiejet. Krakowie, (1) 30:1-12.
1896a. Études Helminthologiques. IV. Amendements et Suppléments au travail de l'auteur sur le Bilharzia polonica sp. nov. Bull. acad. sci. Cracovie, 1896:146-148.
LANG, A.
1880. Untersuchungen zur vergleichenden Anatomie und Histologie des Nervensystems der Platyhelminthen. II. Ueber das Nervensystem der Trematoden. Mitth. Zool. Sta. Neapel, 2:28-52; 3 Taf.
1884. Die Polycladiden des Golfes von Neapel. Fauna u. Flora von Neapel, (2) 11: 1-688; 39 pl.
LANKESTER, E. R.
1901. A Treatise on Zoölogy. IV. The Platyhelmia, Mesozoa, and Nemertini. London. 204 pp.
LA RUE, G. R.
1917. Two New Larval Trematodes from Thamnophis marciana and Thamnophis eques. Occasional Papers Mus. Zool. Univ. Mich., No. 35; 14 pp., 1 pl.
LEBOUR, MARIE V.
1907. Larval Trematodes of the Northumberland Coast. Trans. Nat. Hist. Soc. Northumberland, n.s., 1:437-454; 5 pl.
LEIDY, J.
1877. On Flukes infesting Mollusks. Proc. Acad. Nat. Sci. Phila., 29:200-202.
1890. Notices on Entozoa. Proc. Acad. Nat. Sci. Phila., 42:410-418.
1904. Researches in Helminthology and Parasitology. Smiths. Inst. Misc. Coll. Vol. 46, 281 pp.
LEIPER, R. T.
1915. Report on the Results of the Bilharzia Mission in Egypt, 1915. III. Jour. R. Army Med. Corps, 25:253-267; 15 Figs.
1916. On the Relation between the Terminal-Spined and the Lateral-Spined Eggs of Bilharzia. Brit. Med. Jour., 1916, 1:411.
LEIPER, R. T., and ATKINSON, E. L.
1915. Observations on the Spread of Asiatic Schistosomiasis. Brit. Med. Jour., 1915, 1:201-203; 1 pl.
LEJTENYI, TH.
1881. Ueber den Bau des Gastrodiscus polymastos Leuck. Abhandl. Senkenberg. naturf. Ges. Frankfurt, 12:125-146; 3 Taf.
LEUCKART, R.
1863. Die Menschlichen Parasiten. Leipzig. 766 pp.
1886. Die Parasiten der Menschen. 2 Aufl. 1, Trematodes. Leipzig u. Heidelb. 534 pp.
LEYDIG, FR.
1853. Helminthologische Notizen. Zeit. wiss. Zool., 4:382-384.
LINDNER, E.
1914. Ueber die Spermatogenese von Schistosomum haematobium Bilh. (Bilharzia haematobia Cobb.), mit besonderer Berücksichtigung der Geschlechtschromosomen. Arch. Zellforsch., 12:516-538; 2 Taf.
LINSTOW, O.
1877. Enthelminthologica. Arch. Naturgesch., (1) 43:173-198; 3 Taf.
LOOSS, A.
1885. Beiträge zur Kenntnis der Trematoden. Zeit. wiss. Zool., 41:390-446; 1 Taf.
1892. Ueber Amphistomum subclavatum Rud. Leuckart's Festschr., 142-167; 2 Taf.

1893. Zur Frage nach der Natur des Körperparenchyms bei den Trematoden. Ber. K. Sachs. Ges. wiss., mat.-phys. Cl., Sitz. 9 Jan. 1893, 10-34.

1893a. Ist der Laurer'sche Kanal der Trematoden eine Vagina? Centralbl. Bakt. u. Parasit., Orig. (I) 13:808-819; 4 figs.

1894. Die Distomen unserer Fische und Frösche. Bibl. Zool., 16:1-296; 9 Taf.

1895. Zur Anatomie und Histologie von Bilharzia haematobia (Cobbold). Arch. mikr. Anat., 46:1-108; 3 Taf.

1896. Recherches sur la faune parasitaire de l'Égypte. Première partie. Mém. l'institute Égyptien, 3:1-252; 16 pl.

1899. Weitere Beiträge zur Kenntnis der Trematoden-Fauna Aegyptiens. Zool. Jahrb., Syst., 12:521-784; 9 Taf.

1913. Die Bilharziakrankheit. Handbuch der pathogenen Mikro-organismen, 2 Aufl., Sep. 22 pp.

LORTET, L., ET VIALLETON, L.

1894. Étude sur le Bilharzia et la Bilharziose. Ann. Univ. Lyon, (1) 9, 124 pp., 8 pl. Cited after Looss 1895.

LÜHE, M.

1909. Parasitische Plattwürmer. I. Trematodes. Süsswasserfauna Deutschlands Heft 17. Jena. 218 pp.

LUTZ, A.

1916. Observaçoes sobre a evolucão do Schistosomum mansoni. Nota previa. Brazil Medico, 30:385-387.

MATHEWS, A. P.

1915. Physiological Chemistry. New York. 1040 pp.

MINOT, C. S.

1897. Cephalic Homologies. A Contribution to the Determination of the Ancestry of the Vertebrates. Amer. Nat., 31:927-943.

MIYAIRI, K. UND SUZUKI, M.

1914. Der Zwischenwirt des Schistosomum japonicum Kat. Mitt. med. Fakult. Univ. Kyushu, Fukuoka. 1:187-197; 2 Taf.

MONTGOMERY, R. E.

1906, 1906a. Observations on Bilharziosis among Animals in India. Jour. Trop. Vet. Sci., (1) 1:1-32, (1) 2:1-37; 4 pl.

MONTICELLI, Fr. Sav.

1892. Cotylogaster Michaelis nov. gen., nov. spec. Leuckart's Festschr., pp. 164-214; 2 Tav.

1914. Ricerche sulla Cercaria setifera di Joh. Müller. Ann. Mus. zool. Univ. Napoli, (4) 4:1-49; 5 Tav.

MOULINIÉ, J. J.

1856. De la Reproduction chez les Trematodes Endoparasites. Mém. de l'Inst. Genevois, 3:1-280; 6 pl.

NITZSCH, CH. L.

1807. Seltsame Lebens- und Todesart eines bisher unbekannten Wasserthierchens. Kilian, Georgia. 257-262; 281-286. Cited after Braun 1893.

1816. Beitrag zur Infusorien-kunde der Naturbeschreibung der Zerkarien und Bazillarien. Neue Schrift. Nat. Ges. Halle (1) 3; 1 Taf. Reviewed in Isis, 1818:728

NORDMANN, A. v.

1832. Mikrographische Beiträge. I. Berlin. 118 pp., 10 Taf.

ODHNER, T.

1907. Zur Anatomie der Didymozoen: ein getrenntgeschlechtlicher Trematode mit rudimentären Hermaphroditismus. Zool. Studien Tullberg, 1907:309-342; 1 Taf.

1910. Gigantobilharzia acotylea, n.g., n.sp., ein mit den Bilharzien verwandter Blutparasit von enormer Lange. Zool. Anz., 35:380-385; 5 Figs.

1911. Zum natürlichen System der digenen Trematoden. 1. Zool. Anz., 37:181-191.
1912. Zum natürlichen System der digenen Trematoden. V. Zool. Anz., 41:54-71; 7 Figs.

PAGENSTECHER, H. A.
1857. Trematodenlarven und Trematoden. Heidelb. 56 pp., 6 Taf.

PARONA, C., E ARIOLA, V.
1896. Bilharzia Kowalewskii n. sp. nel Larus melanocephalus. Boll. Mus. Zool. e Anat. Comp. Univ. Genova, 45:1-3.

POIRIER, J.
1886. Trématodes nouveaux ou peu connus. Bull. Soc. philomath. Paris. Seance du 28 Nov. 1885. 21 pp. 4 pl.

PRATT, H. S.
1909. The Cuticula and Subcuticula of the Trematodes and Cestodes. Amer. Nat., 43:705-729; 12 Figs.

RETTGER, L. J.
1897. Some Additions to our Knowledge of the Anatomy and Embryology of the Holostomidae. Proc. Ind. Acad. Sci., 1896:224, 225.

REUSS, H.
1903. Beobachtungen an der Sporocyst und Cercaria des Distomum duplicatum. Zeit. wiss. Zool., 74:458-477; 1 Taf.

ROSSBACH, E.
1906. Beiträge zur Anatomie und Entwicklungsgeschichte der Redien. Zeit. wiss Zool., 84:361-445; 4 Taf.

ROSSETER, T. B.
1909. On Holostomum excisum (Linstow, 1906) and the Development of the Tetracotyliform Larva to a Holostomum sp. Jour. Quek. Micr. Club, (2) 10:385-392; 1 pl.

RUDOLPHI, C. A.
1819. Entozoorum Synopsis. Berlin. 812 pp.

SCHAUINSLAND, H.
1883. Beiträge zur Kenntnis der Embryonalentwicklung der Trematoden. Jenai. Zeit. Naturwiss., 16:465-527; 3 Taf.

SCHMARDA, L. K.
1871. Zoologie. Vol. I. Wien. 372 pp.

SCHNEIDER, A.
1864. Ueber die Muskeln der Würmer und ihre Bedeutung für das System. Arch. Anat. Physiol., 1864:590-597.

SCHULZE, M.
1853. Zoölogische Skizzen. Zeit. wiss. Zool., 4:178-195.

SCHWARZE, W.
1886. Die postembryonale Entwicklung der Trematoden. Zeit. wiss. Zool., 43:41-86; 1 Taf.

SIEBOLD, TH. v.
1835. Helminthologische Beiträge. I. Arch. Naturgesch., (1) 1:45-83; 1 Taf.

SSINITZIN, D. TH.
1905. Distomes des poissons et des grenouilles des environs de Varsovie. Materiaux pour l'histoire naturelle des Trématodes Mém. soc. nat. Varsovie. Biol., 15:1-210, 6 pl. Russian.
1910. Studien über die Phylogenie der Trematoden. Biol. Zeit., 1:1-63; 2 Taf.
1911. La génération parthénogénétique des Trématodes et sa descendance dans les mollusques de la Mer Noire. Mém. Acad. Sci. St. Petersbourg, (8) 30:1-127; 6 pl. Russian.

STEENSTRUP, J. J. S.
1842. Ueber den Generationswechsel oder die Fortpflanzung und Entwicklung durch abwechselnde Generationen. Copenh. 60 pp.
STILES, CH. W., and HASSALL, A.
1908. Index Catalog of Medical and Veterinary Zoölogy. Trematoda and Trematode Diseases. U. S. Hyg. Lab. Bull. 37. 401 pp.
SURFACE, F. M.
1907. The Early Development of the Polyclad, Planocera inquilina. Proc. Acad. Nat. Sci. Phila., 59:514-559; 6 pl.
TENNENT, D. H.
1906. A Study of the Life History of Bucephalus haimaenus: a Parasite of the Oyster. Quart. Jour. Micr. Sci., n.s., 49:99-133; 2 pl.
THOMAS, A. P.
1883. Life History of the Liver Fluke. Quart. Jour. Micr. Sci., 23:99-133; 2 pl.
THOSS, E.
1897. Ueber den Bau von Holostomum cucullus nov. spec. Leipzig. 66 pp., 2 Taf.
WARD, H. B.
1909. Fasciolopsis buskii, F. Rathouisi, and Related Species in China. Trans. Amer. Micr. Soc., 29:5-16; 2 pl.
1916. Notes on Two Free-Living Larval Trematodes from North America. Jour. Parasit., 3:10-20; 1 pl.
WRIGHT, S.
1912. Notes on the Anatomy of Microphallus opacus. Trans. Amer. Micr. Soc., 31: 167-176; 2 pl.
ZAILER, O.
1914. Zur Kenntnis der Anatomie der Muskulatur und des Nervensystem der Trematoden. Zool. Anz., 44:385-396; 3 Figs.

EXPLANATION OF PLATES

ABBREVIATIONS

ad	anterior dorsalis nerve	ne	nerrve ending
al	anterior lateralis nerve	np	nervus palatinus
as	anterior sensory field	nph	pharyngealis nerve
av	anterior ventralis nerve	ns	subesophageal commissure
b, bc	genital atrium	nt	nerve trunk
bl	bursa glands	o	ovum
br	cerebral ganglion	od	oviduct
c, ce	cecum	on	oral nerve ring
ca	caudal pocket	op	optic nerve cell
ceg	cercaria germ-ball	opc	optic cup
cg	caudal gland cells	opn	optic nerve
cr	cirrus pouch	or	oral sucker
cs	collar spines	ot	ootype
d, dl	salivary gland duct	ov	ovary
dc	dorsal commissure	p	pharynx
dlc	dorsolateral commissure	pa	parenchyma
dp	profundus of dorsalis nerve	pb	polar body
ds	superficialis of dorsalis nerve	pc	preacetabular commissure
e	epithelium	pd	posterior dorsalis nerve
ec	ectoderm	pe	preoral sense endings
eg	excretory granules	pg	primitive genital pore
eh	evertible prepharynx	pgl	locomotor pocket glands
ep	excretory pore	pl	posterior lateralis nerve
es	esophagus	po	postacetabular commissure
et	excretory tube	pv	posterior ventralis nerve
ev	excretory vesicle	pvc	postero-ventrolateralis commissure
ex	excretory tubule	pvi	postero-ventral intermedius nerve
fc	flame cell	r	rhabdocoel gut
g	genital pore, birth pore	rm	ramus muscularis of the lateralis nerve
gb	germ-ball	rp	ramus palpalis of the lateralis nerve
glc	cystogenous cell	sg	salivary gland cell
i	intermedius nerve	sp	acetabular spine
igl	digestive gland	st	stylet
l	longitudinal muscle cell	t	basement membrane
lc	Laurer's canal	te, $t_{1,2}$	testis
le	lateral eye	tr	transverse muscle fiber
lg	localized germinal epithelium	u	uterus
lp	posterior locomotor pocket	v	vagina
ls	lateral suctorial groove	vd	vas deferens
m	myoblast	ve	vas efferens
me	median eye-spot	vf	vitelline follicles
mp	musculus preoralis	vi	vitelline duct
n, nc	nerve cell	vs	acetabulum

The lines in figures 6, 26, 51, 146, 147 have a value of 0.5mm; in figures 5, 7, 13-17, 19-20, 27-29, 31-34, 36, 37, 44-46,54, 56, 57, 61, 68-75, 77, 82, 83, 89, 91, 92, 97-99, 101, 102, 104, 107, 108, 111-113, 118, 119, 121-133, 136, 138, 140, 141, 145, 150-154, a value of 0.01 mm; in all other figures, a value of 0.05 mm.

PLATE I

DESCRIPTION OF PLATE

Figs. 1-3.—*Cercaria pellucida*; sketches of progressive stages of pigmentation; dorsal view, showing two lateral eye-spots and one median spot. × 100.

Fig. 4.—*Cercaria pellucida*; dorsal view, somewhat contracted. × 100.

Fig. 5.—*Cercaria pellucida*; anterior tip, figuring details of pigmentation and contents of the excretory tube. × 330.

Fig. 6.—*Cercaria pellucida*; redia, characterized by extensive rhabdocoel gut and spinous prepharynx. × 34.

Fig. 7.—*Cercaria pellucida*; detail of the spinous prepharynx of the redia. × 540.

Fig. 8.—*Cercaria pellucida*; young redia; precocious development of the cercariae before the redia is mature. × 38.

Figs. 9-11.—*Cercaria pellucida*; three stages in encystment. × 38.

Fig. 12.—Young *Cercaria pellucida*; origin of posterior locomotor pockets within the caudal pocket. × 170.

Fig. 13.—*Cercaria pellucida*; transverse section thru the middle of the body. × 330.

Fig. 14.—*Cercaria pellucida*; detail of cystogenous gland cells in the region of the lateral eye-spot. × 330.

Fig. 15.—*Cercaria pellucida*; contracted excretory bladder and posterior locomotor pockets. × 238.

Figs. 16, 17.—*Cercaria pellucida*; details of the posterior locomotor pocket; Fig. 16, contracted; Fig. 17, relaxed; *xx*, retractor muscles; *yy*, reflexor muscles. × 540.

Fig. 18.—The genitalia of *Cercaria pellucida*; regions of ootype and metraterm. × 238.

Fig. 19.—*Cercaria pellucida*; transverse section thru tail, indicating arrangement of ordinary parenchyma cells. × 540.

Fig. 19a.—*Cercaria pellucida*; oblique section thru tail, indicating arrangement of muscle fibers. × 540.

PLATE I

DESCRIPTION OF PLATE

Figs. 1-3.—*Cercaria pellucida*; sketches of progressive stages of pigmentation; dorsal view, showing two lateral eye-spots and one median spot. × 100.

Fig. 4.—*Cercaria pellucida*; dorsal view, somewhat contracted. × 100.

Fig. 5.—*Cercaria pellucida*; anterior tip, figuring details of pigmentation and contents of the excretory tube. × 330.

Fig. 6.—*Cercaria pellucida*; redia, characterized by extensive rhabdocoel gut and spinous prepharynx. × 34.

Fig. 7.—*Cercaria pellucida*; detail of the spinous prepharynx of the redia. × 540.

Fig. 8.—*Cercaria pellucida*; young redia; precocious development of the cercariae before the redia is mature. × 38.

Figs. 9-11.—*Cercaria pellucida*; three stages in encystment. × 38.

Fig. 12.—Young *Cercaria pellucida*; origin of posterior locomotor pockets within the caudal pocket. × 170.

Fig. 13.—*Cercaria pellucida*; transverse section thru the middle of the body. × 330.

Fig. 14.—*Cercaria pellucida*; detail of cystogenous gland cells in the region of the lateral eye-spot. × 330.

Fig. 15.—*Cercaria pellucida*; contracted excretory bladder and posterior locomotor pockets. × 238.

Figs. 16, 17.—*Cercaria pellucida*; details of the posterior locomotor pocket; Fig. 16, contracted; Fig. 17, relaxed; *xx*, retractor muscles; *yy*, reflexor muscles. × 540.

Fig. 18.—The genitalia of *Cercaria pellucida*; regions of ootype and metraterm. × 238.

Fig. 19.—*Cercaria pellucida*; transverse section thru tail, indicating arrangement of ordinary parenchyma cells. × 540.

Fig. 19a.—*Cercaria pellucida*; oblique section thru tail, indicating arrangement of muscle fibers. × 540.

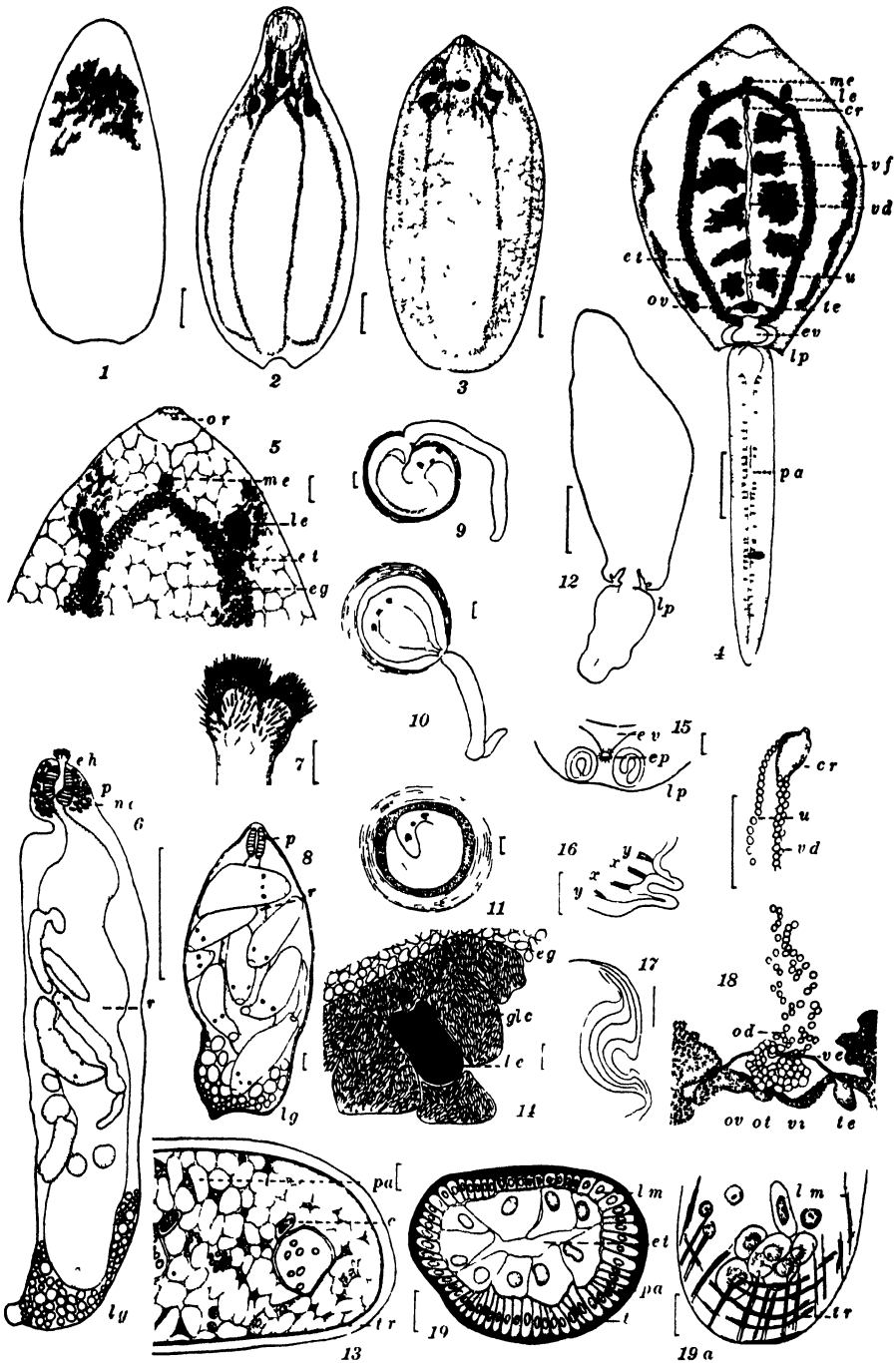

1
2
3
me
le
cr
vf
vd
et
u
ov
te
ev
lp
pa
4
or
5
me
le
et
eg
9
12
lp
10
7
ev
15
ep
lp
cr
u
vd
eh
p
nc
6
r
lg
p
8
r
lg
11
16
y
x
y
eg
glc
lc
14
17
18
od
ve
ov
ot
vi
te
pa
c
tr
13
lm
et
pa
t
19
lm
tr
19 a

PLATE II

DESCRIPTION OF PLATE

Fig. 20.—*Cercaria pellucida*; sagittal section thru pharynx and gut of redia, with prepharynx organ retracted. × 330.

Fig. 21.—*Cercaria pellucida*; transverse section thru body in region of posterior locomotor pocket glands. × 170.

Fig. 22.—*Cercaria pellucida*; optical view of the proliferation of the germ-balls from the posterior germinal epithelium of the redia. × 330.

Fig. 23.—*Cercaria pellucida*; central nervous system, typical for the trioculate species of monostome cercariae. × 330.

Fig. 24.—Young *Cercaria pellucida*; oblique section thru ganglion mass, showing connection of eye-spots with brain center. × 330.

Fig. 25.—*Cercaria konadensis*; dorsal view. × 105.

Fig. 26.—Redia of *Cercaria konadensis*. × 34.

Fig. 27.—*Cercaria konadensis*; detail of paired group of caudal gland cells. × 540.

Fig. 28.—*Cercaria konadensis*; genital cell masses in region of ootype. × 540.

Fig. 29.—*Cercaria konadensis*; detail of excretory bladder and posterior locomotor pockets. × 238.

Fig. 30.—*Cercaria konadensis*; optical view of the germinal rachis of the redia. × 330.

Fig. 31.—*Cercaria konadensis*; sagittal section thru aspinose prepharynx of the redia. × 330.

Fig. 32.—Mature *Cercaria urbanensis* Cort; transverse section thru tail, showing caudal gland cells. × 330.

Figs. 33, 34.—*Cercaria urbanensis*; stages in differentiation of caudal gland cells from ordinary parenchyma cells. × 330.

Fig. 35.—*Cercaria urbanensis*; detail of excretory vesicle and posterior locomotor pockets. × 238.

Fig. 36.—Early germ-balls of *Cercaria urbanensis*; oblique section thru brain mass and lateral eye-spot, showing ectodermal origin of pigment cup, and connection with optic cells of brain. × 730.

Fig. 37.—Oblique longitudinal section thru *Cercaria pellucida*, showing detail of nerve endings. × 730.

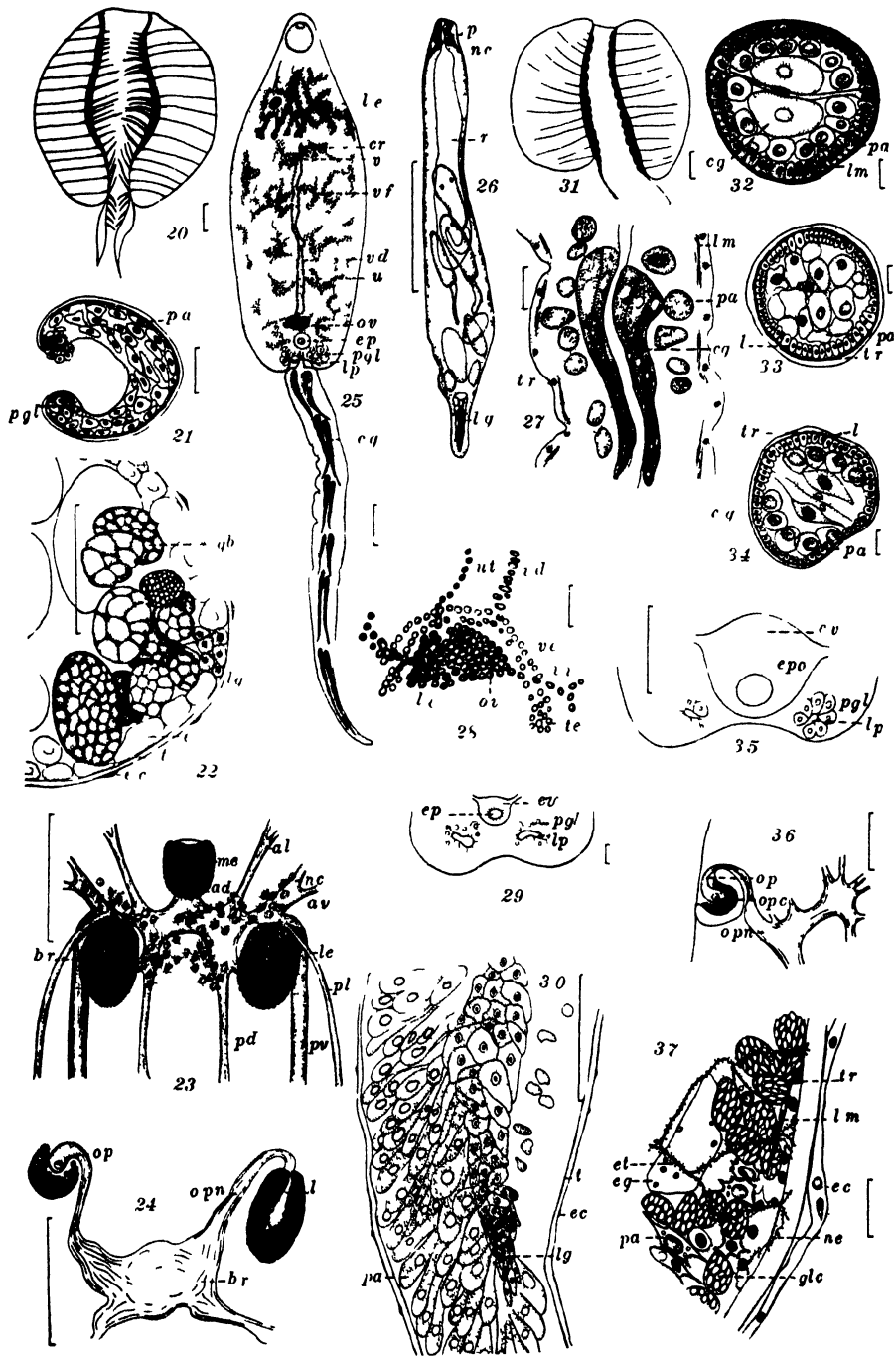

20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
le
cr
v
vf
vd
u
ov
ep
pgl
lp
cg
p
nc
r
lg
pa
lm
tr
l
gb
ut
vi
ve
ov
te
cv
epo
pgl
lp
ep
ev
me
al
ad
nc
av
br
le
pl
pd
pv
op
opn
l
t
ec
lg
opc
et
eg
ne
glc

PLATE III

DESCRIPTION OF PLATE

Fig. 38.—*Cercaria flabelliformis*; ventral view of worm freed from cyst; *ll*, lateral lappets × 80.

Fig. 39.—*Cercaria flabelliformis*; dorsal view, giving details of the excretory system and genitalia. × 80.

Fig. 40.—*Cercaria flabelliformis*; lateral view, showing suctorial cup in anterior portion of worm; *ll*, lateral lappets. × 80.

Fig. 41.—Immature *Cercaria flabelliformis* within cyst. × 54.

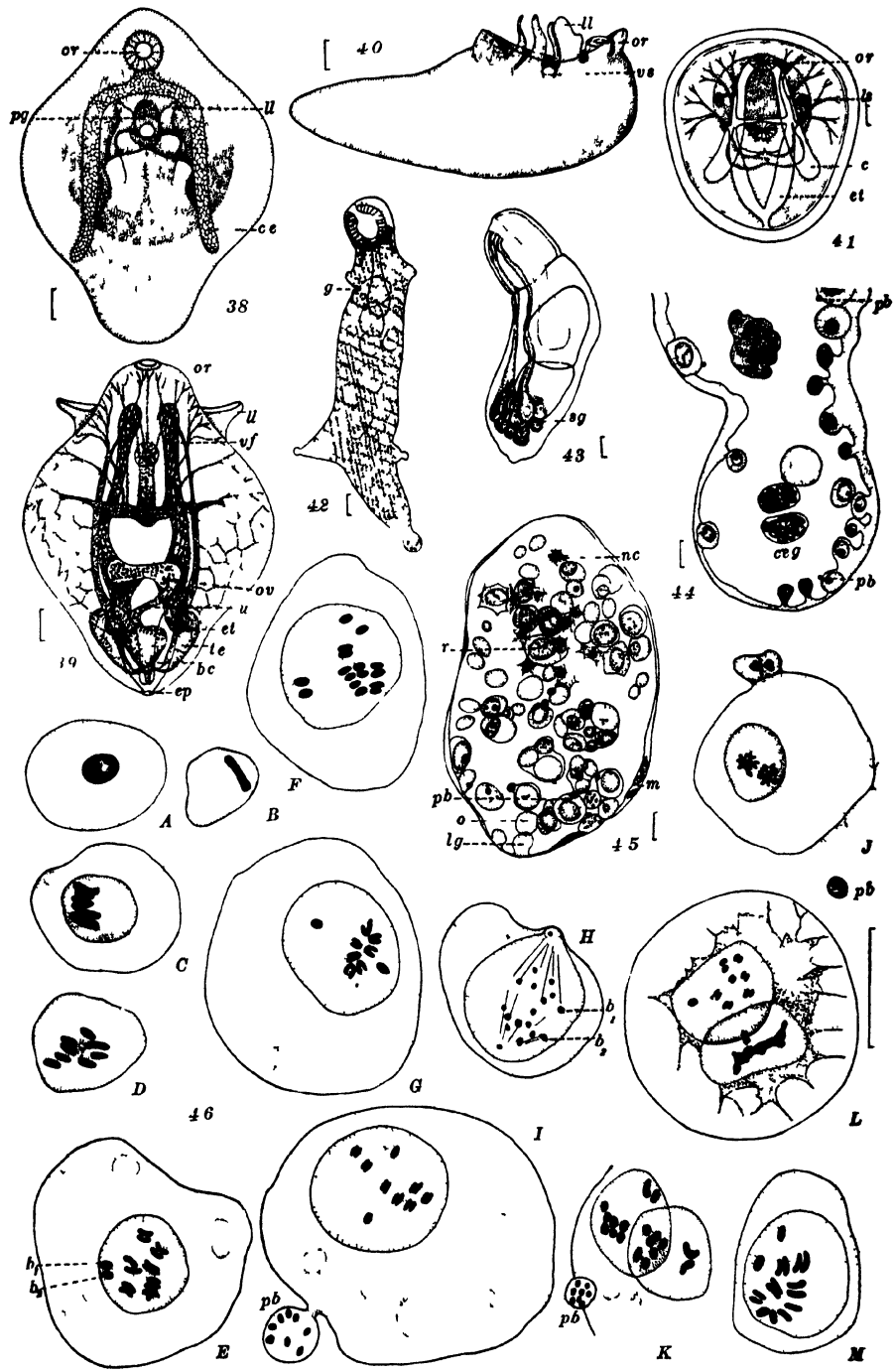
Fig. 42.—*Cercaria flabelliformis*; young redia, detailing the excretory channels in the worm. × 54.

Fig. 43.—*Cercaria flabelliformis*; redia showing paired salivary glands emptying into the oral pocket. × 54.

Fig. 44.—*Cercaria flabelliformis*; mid-frontal section thru young daughter redia in region of germinal cell maturation. × 330.

Fig. 45.—*Cercaria flabelliformis*; median frontal section thru young daughter redia, showing proliferation of germinal epithelium at posterior end of gut. × 330.

Fig. 46 a-m.—*Cercaria flabelliformis* rediae; maturation of parthenogenetic ova; *A*, resting cell; *B*, *C*, formation of spireme; *D*, division of spireme skein into eight chromosomes; *E*. *F*, *G*, longitudinal splitting of chromosomes at equatorial plate; *H*, mitosis, with forma. tion of polar body and preparation of ovum for second mitosis; *I*, polar body almost constricted off, chromosome *b* excentric; *J*, ovum preparing for second division, polar body also dividing; *K*, cell cleavage, with precocious chromosomes b_1, b_2 excentric; *L*, first cleavage of a cercaria-ovum, with polar body degenerating; *M*, metaphase of a somatic cell in process of division. × 1620.



FAUST LIFE HISTORY OF TREMATODES PLATE III

PLATE IV

DESCRIPTION OF PLATE

Fig. 47.—*Tetracotyle pipientis*; ventral view, showing digestive tract and genital system. × 105.

Fig. 48.—*Tetracotyle pipientis*; diagram of the excretory system, with excretory granular inclusions. × 105.

Fig. 49.—*Cercaria ptychocheilus*; ventral view, including digestive, excretory and genital systems. × 105.

Fig. 50.—*Cercaria ptychocheilus*; sketch of encysted worm. × 25.

Fig. 51.—*Cercaria ptychocheilus*; sketch of ruptured cyst with attachment annulus. × 25.

Fig. 52.—*Cercaria ptychocheilus*; detail of genital system. × 165.

Fig. 53.—*Cercaria ptychocheilus*; nervous system. × 330.

Fig. 54.—*Cercaria ptychocheilus*; transverse section thru middle of body. × 540.

Fig. 55.—*Cercaria crenata*; dorsal view. × 170.

Figs. 56, 57.—*Cercaria crenata*; ventral and lateral views of stylet. × 540.

Fig. 58.—*Cercaria crenata*; sporocyst. × 54.

Fig. 59.—*Cercaria crenata*; detail of genitalia. × 170.

Fig. 60.—*Cercaria glandulosa*; ventral view. × 370.

Fig. 61.—*Cercaria glandulosa*; ventral view of stylet. × 370.

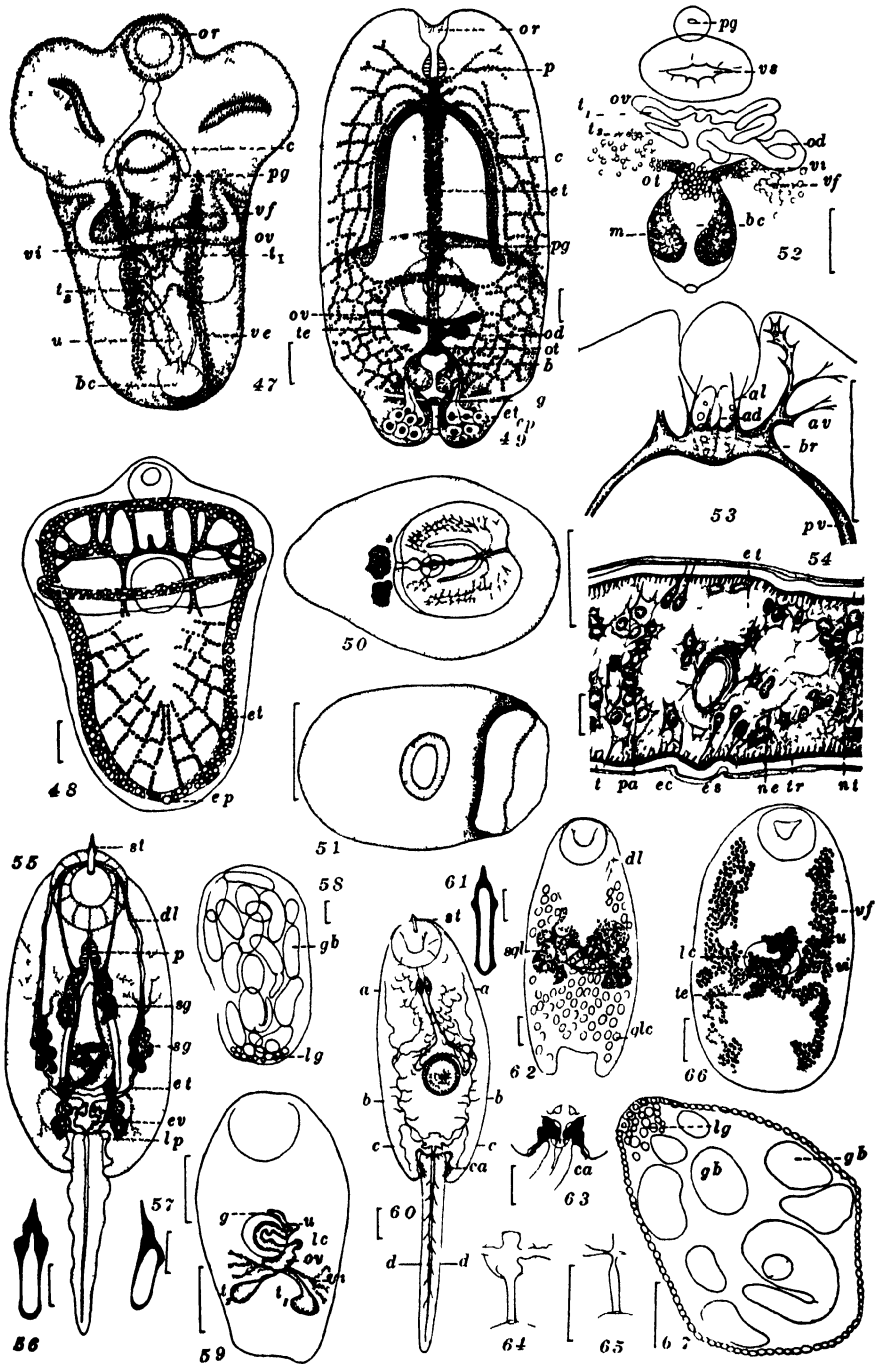
Fig. 62.—*Cercaria glandulosa*; salivary and cystogenous glands. × 75.

Fig. 63.—*Cercaria glandulosa*; detail of caudal pockets, showing insertion of tail, spinose lateral grooves, and three-spined ventral flap. × 100.

Figs. 64, 65.—*Cercaria glandulosa*; outline of excretory vesicle, open and closed. × 200.

Fig. 66.—*Cercaria glandulosa*; genital cell masses, dorsal view. × 110.

Fig. 67.—*Cercaria glandulosa*; sporocyst. × 170.



FAUST LIFE HISTORY OF TREMATODES PLATE IV

PLATE V

DESCRIPTION OF PLATE

Figs. 68-70.—*Cercaria glandulosa*; consecutive frontal sections, giving details of the nervous system anterior to the brain. × 540.

Fig. 71.—*Cercaria glandulosa*; frontal section, with details of innervation of acetabulum. × 540.

Fig. 72-75.—*Cercaria glandulosa*; transverse sections thru levels *aa* to *dd* of Fig. 60. × 540.

Fig. 76.—*Cercaria diaphana*; ventral view, considerably flattened by cover slip. × 170.

Fig. 77.—*Cercaria diaphana*; ventral view of stylet. × 540.

Fig. 78.—*Cercaria diaphana*; ventral view, giving details of glands and genital cell masses. × 170.

Figs. 79, 80.—*Cercaria diaphana*; sporocysts. × 80.

Fig. 81.—*Cercaria dendritica*; ventral view. × 170.

Figs. 82, 83.—*Cercaria dendritica*; lateral and ventral views of stylet. × 250.

Fig. 84.—*Cercaria dendritica*; encysted worm. × 150.

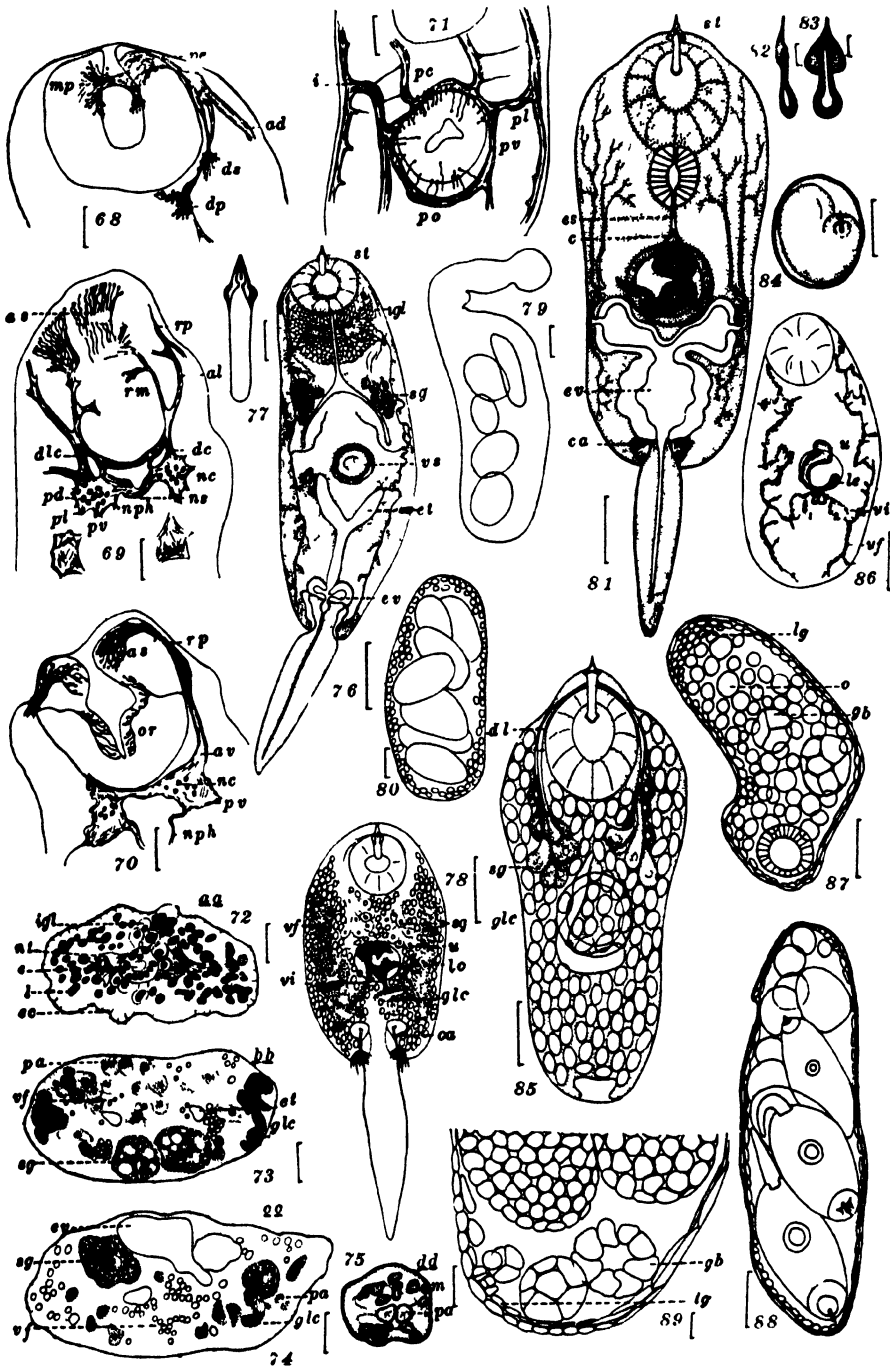
Fig. 85.—*Cercaria dendritica*; salivary and cystogenous glands. × 170.

Fig. 86.—*Cercaria dendritica*; genital system. × 150.

Fig. 87.—*Cercaria dendritica*; young sporocyst. × 150.

Fig. 88.—*Cercaria dendritica*; mature sporocyst. × 150.

Fig. 89.—*Cercaria dendritica*; posterior end of mature sporocyst, showing origin of germ-balls from localized germinal epithelium. × 330.



FAUST LIFE HISTORY OF TREMATODES PLATE V

PLATE VI

DESCRIPTION OF PLATE

Fig. 90.—*Cercaria micropharynx*; ventral view. × 170.
Figs. 91, 92.—*Cercaria micropharynx*; ventral and lateral views of stylet. × 540.
Fig. 93.—*Cercaria micropharynx*; distribution of glands. × 170.
Fig. 94.—*Cercaria micropharynx*; sporocyst with non-localized germinal epithelium. ×
Fig. 95.—*Cercaria micropharynx*; cercariae encysted in old sporocyst. × 54.
Fig. 96.—*Cercaria micropharynx*; genital cell masses. × 170.
Fig. 97.—*Cercaria micropharynx*; transverse section thru brain center. × 540.
Fig. 98.—*Cercaria micropharynx*; transverse section thru excretory cornua. × 540.
Fig. 99.—*Cercaria micropharynx*; transverse section thru tail. × 540.
Fig. 100.—*Cercaria racemosa*; ventral view. × 150.
Figs. 101, 102.—*Cercaria racemosa*; ventral and lateral views of stylet. × 330.
Fig. 103.—*Cercaria racemosa*; detail of salivary glands. × 150.
Fig. 104.—*Cercaria racemosa*; genital cell masses. × 330.
Figs. 105, 106.—*Cercaria racemosa*; sporocysts, showing localized germinal epithelium and attachment organ, *ao*. × 54.
Fig. 107.—*Cercaria racemosa*; lateral view of genital cell masses in region of acetabulum. × 330.
Fig. 108.—*Cercaria racemosa*; optical view of the sporocyst in region of birth-pore, *bp*; arrow points toward attachment organ. × 330.
Fig. 109.—*Cercaria trisolenata*; ventral view. × 150.
Fig. 110.—*Cercaria trisolenata*; dorsal view of collar spines. × 170.
Fig. 111.—*Cercaria trisolenata*; lateral view of collar spines. × 330.
Fig. 112.—*Cercaria trisolenata*; sketch of acetabular spines. × 540.
Fig. 113.—*Cercaria trisolenata*; typical cystogenous cell glands, showing granules and chromidia. × 540.
Fig. 114*A-E*.—*Cercaria trisolenata*; sketches of developmental stages. × 80.
Fig. 115 *A-C*.—*Cercaria trisolenata*; stages in encystment. × 80.

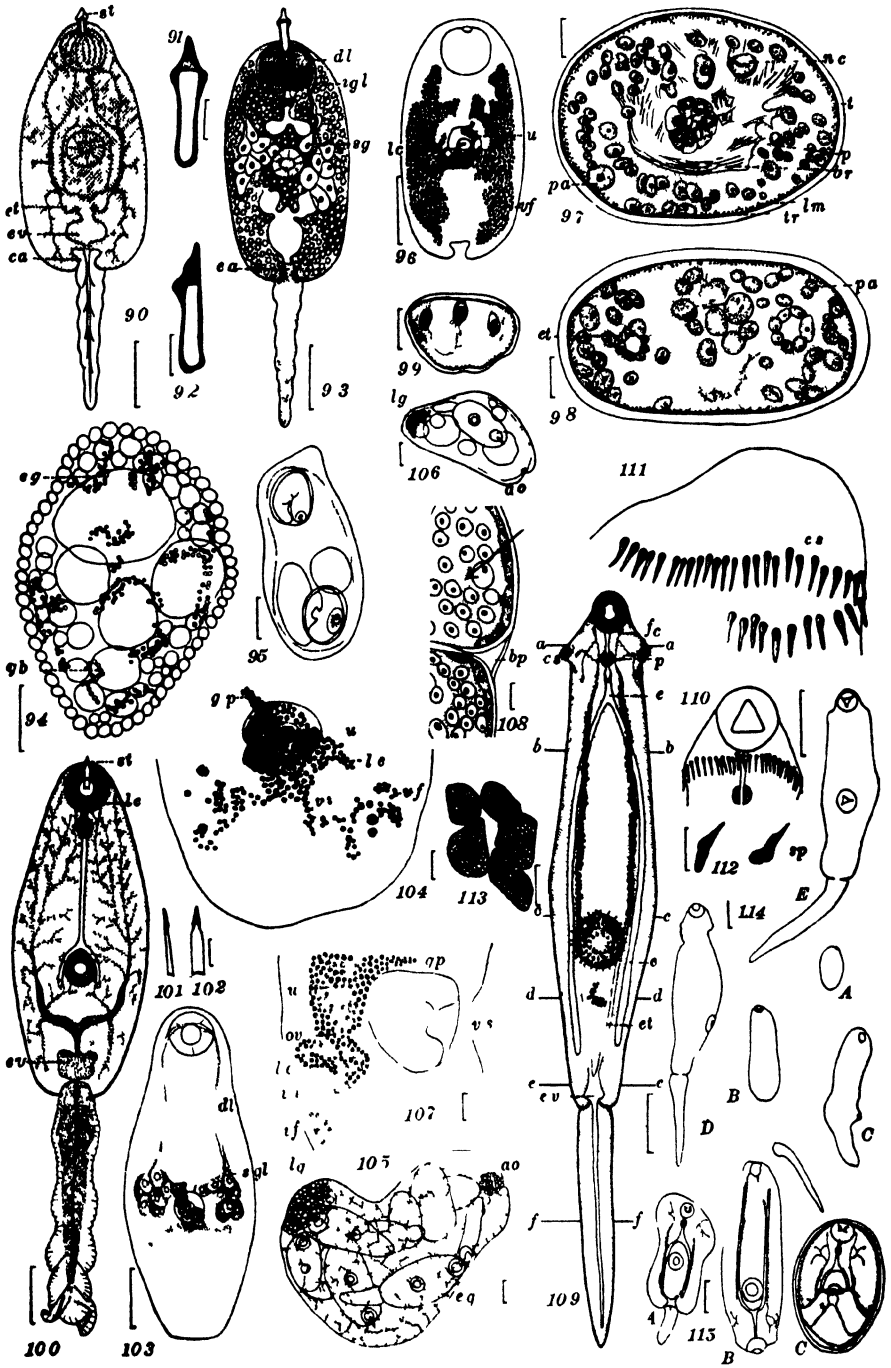

90
91
92
93
96
97
98
99
100
101 102
103
104
106
107
108
109
110
111
112
113
114
115
A
B
C
D
E

PLATE VII

DESCRIPTION OF PLATE

Fig. 116.—*Cercaria trisolenata*; encysted worm. × 150.
Fig. 117.—*Cercaria trisolenata*; redia. × 50.
Fig. 118.—*Cercaria trisolenata*; longitudinal and transverse muscle fibers of the digestive tract, showing myoblast connections. × 730.
Fig. 119.—*Cercaria trisolenata*; peripheral muscle fibers of longitudinal system. × 730.
Fig. 120.—*Cercaria trisolenata*; genital cell masses. × 220.
Fig. 121.—*Cercaria trisolenata*; butterfly stage in development of the central nervous system. × 330.
Fig. 122.—*Cercaria trisolenata*; differentiating stage in development of central nervous system. × 330.
Figs. 123, 124.—*Cercaria trisolenata*; lateral and dorsal views of central nervous system of mature cercaria. × 330.
Fig. 125.—*Cercaria trisolenata*; central nervous system of the redia. × 220.
Fig. 126.—*Cercaria trisolenata*; distribution of nerve cells in the redia, median sagittal section. × 330.
Fig. 127.—*Cercaria trisolenata*; detail of the peripheral nerves of the redia. × 540.
Figs. 128-133.—*Cercaria trisolenata*; transverse sections at levels *aa* to *ff* of Fig. 109. × 330.

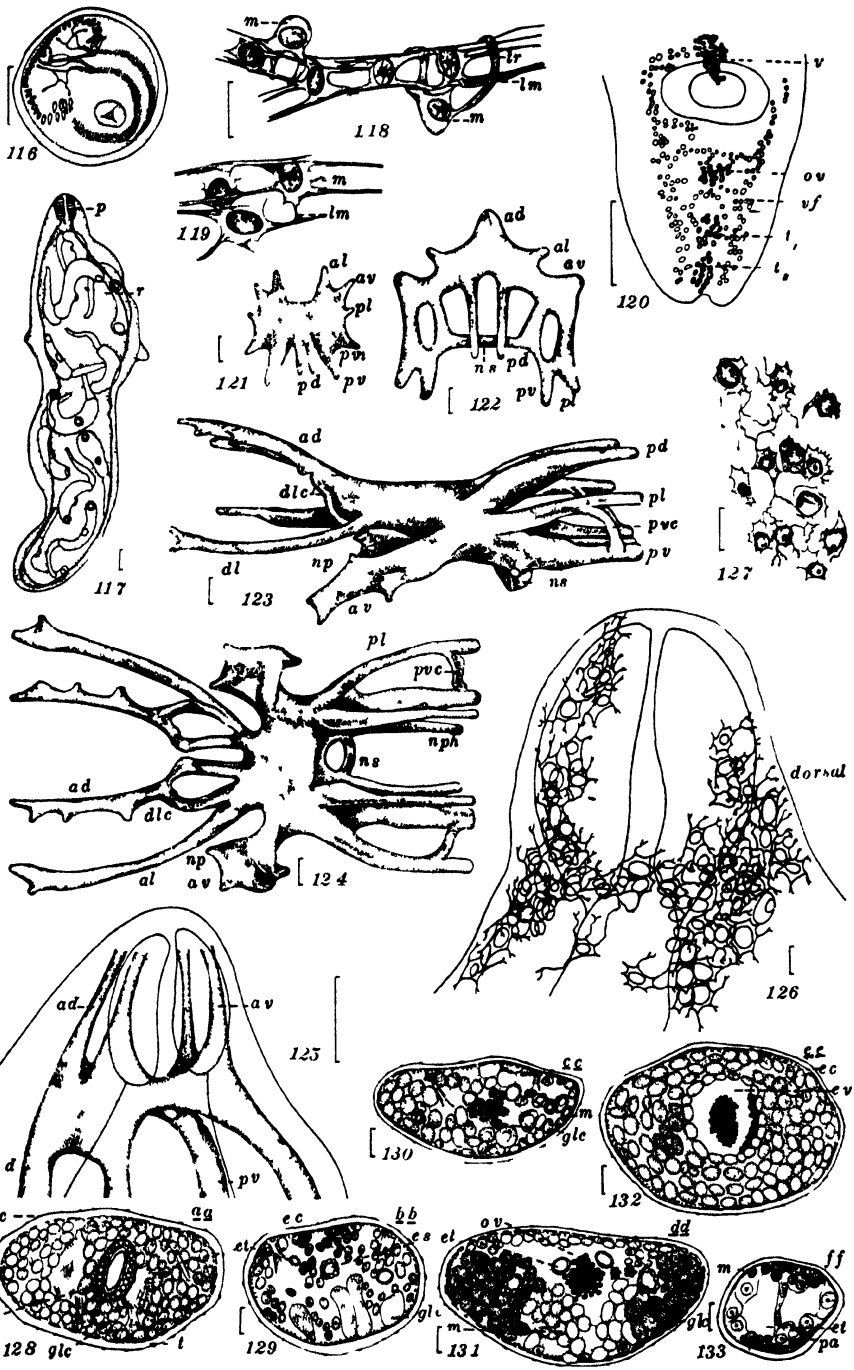
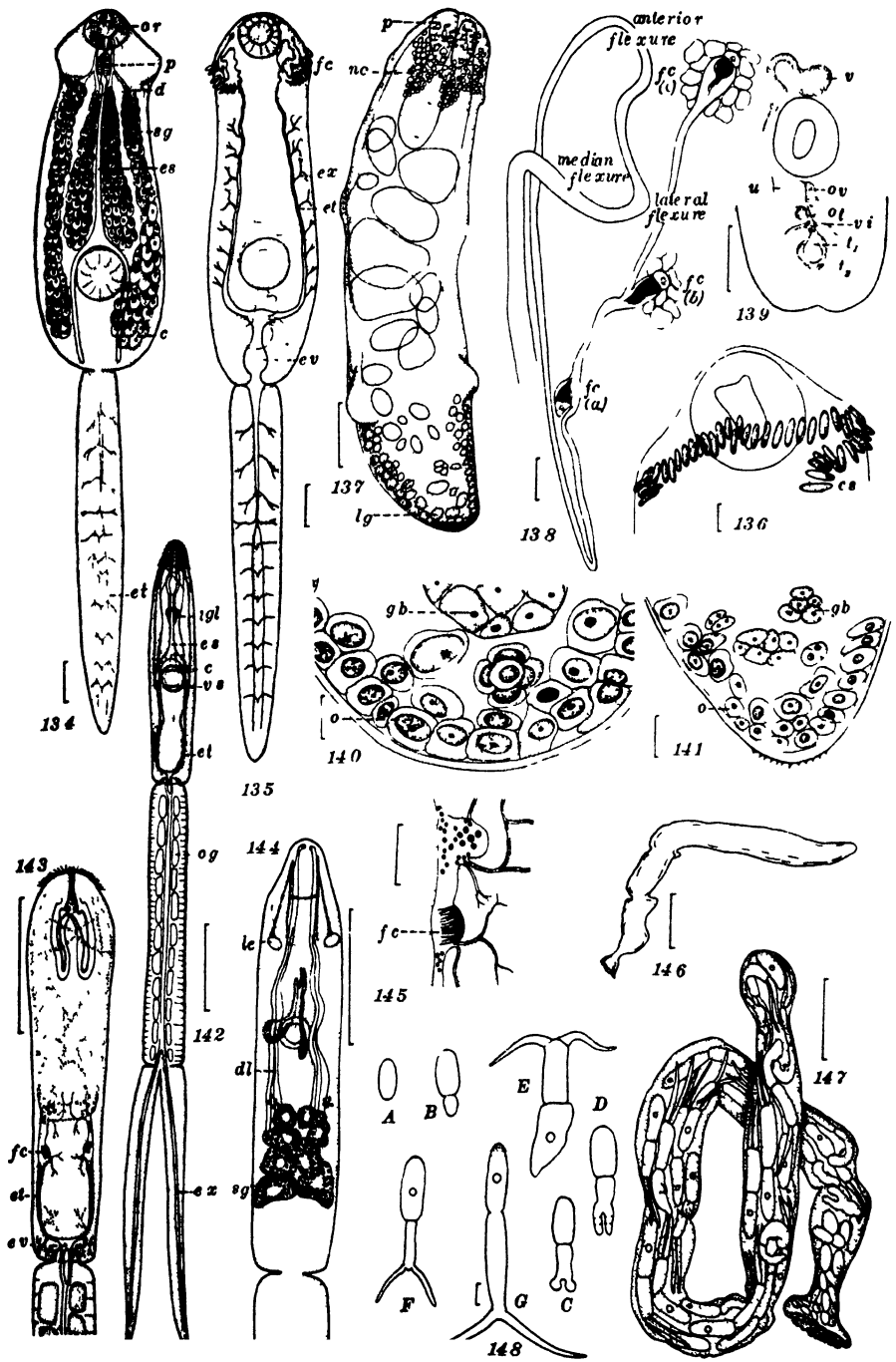

116
m
lr
lm
m
118
v
ov
vf
120
m
lm
119
p
r
117
al
av
pl
pvi
pd
pv
121
ad
al
av
ns
pd
pv
pl
122
ad
dlc
pd
pl
pvc
pv
dl
np
ns
av
123
127
pl
pvc
nph
ns
ad
dlc
np
al
av
124
dorsal
126
ad
av
125
pd
pv
cc
m
glc
130
cc
ec
ev
132
ec
aa
p
glc
t
128
ec
bb
et
es
glc
129
et
ov
dd
m
glc
131
m
ff
et
pa
133

PLATE VIII

DESCRIPTION OF PLATE

Fig. 134.—*Cercaria biflexa*; ventral view, showing salivary gland cells. × 105.
Fig. 135.—*Cercaria biflexa*: ventral view, showing excretory system. × 105.
Fig. 136.—*Cercaria biflexa*; lateral view of collar spines. × 330.
Fig. 137.—*Cercaria biflexa*; redia of worm. × 170.
Fig. 138.—*Cercaria biflexa*; detail of three flame cells in cephalic region. × 540.
Fig. 139.—*Cercaria biflexa*; genital cell masses. × 170.
Fig. 140.—*Cercaria trisolenata*; posterior end of redia. × 540.
Fig. 141.—*Cercaria biflexa*; posterior end of redia. × 540.
Fig. 142.—*Cercaria gracillima*; ventral view. × 230.
Fig. 143.—*Cercaria gracillima*; excretory system. × 350.
Fig. 144.—*Cercaria gracillima*; dorsal view of trunk, showing eye-spots and salivary glands × 350.
Fig. 145.—*Cercaria gracillima*; detail of flame cell of excretory system. × 750.
Figs. 146, 147.—*Cercaria gracillima*; sporocysts; Fig. 146, x 14; Fig. 147, × 21.
Fig. 148 *A-G*.—*Cercaria gracillima*; stages in development. × 50.

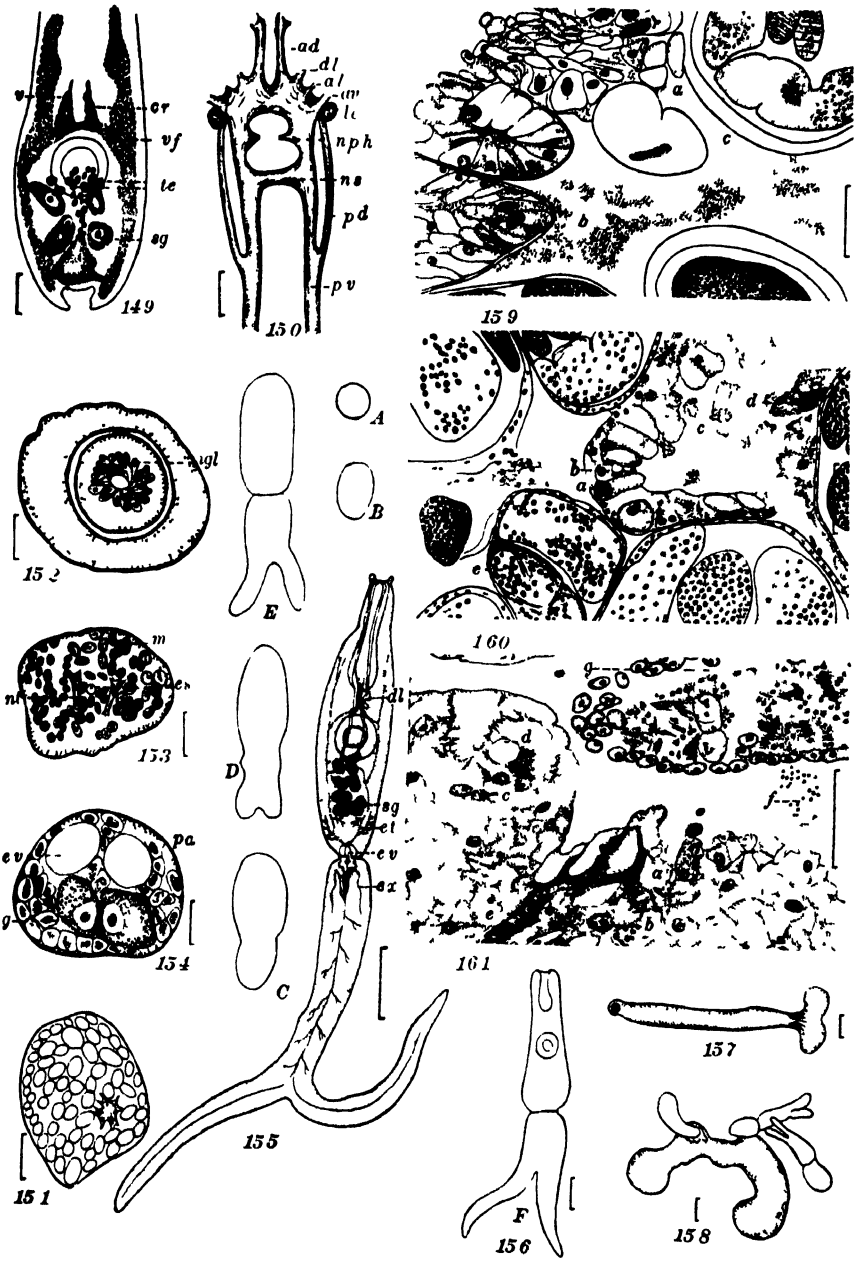


FAUST LIFE HISTORY OF TREMATODES PLATE VIII

PLATE IX

DESCRIPTION OF PLATE

Fig. 149.—*Cercaria gracillima*; genital cell masses. × 270.
Fig. 150.—*Cercaria gracillima*; nervous system. × 540.
Fig. 151.—*Cercaria gracillima*; central nervous system in a very young germ-ball. × 540.
Fig. 152.—*Cercaria gracillima*; transverse section thru esophagus glands. × 540.
Fig. 153.—*Cercaria gracillima*; transverse section thru region slightly posterior to that shown in Fig. 152. × 540.
Fig. 154.—*Cercaria gracillima*; transverse section thru salivary glands. × 540.
Fig. 155.—*Cercaria tuberistoma*; ventral view. × 170.
Fig. 156 *A-F*.—*Cercaria tuberistoma*; stages in development. × 75.
Figs. 157, 158.—*Cercaria tuberistoma*; sporocysts. × 54.
Fig. 159.—*Cercaria biflexa*; section thru liver tissue of *Physa gyrina* Say, showing infection; *a*, disintegrating cecum; *b*, broken down connective tissue; *c*, section of worm. × 170.
Fig. 160.—*Cercaria micropharynx*; section thru liver tissue of *Lymnaea proxima* Lea, infected with the worm; *a*, fatty bodies in degenerating cecum; *b*, vacuoles; *c*, sloughing tissue; *d*, karyolysis; *e*, section of worm. × 170.
Fig. 161.—*Cercaria gracillima*; section thru liver tissue of *Physa gyrina* Say infected with the worm; *a*, cytolysis; *b*, fatty globules; *c*, karyolysis; *d*, vacuoles; *e*, fibromata; *f*, sand inclusions; *g*, section of worm. × 240.



FAUST LIFE HISTORY OF TREMATODES PLATE IX

ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. IV October, 1917 No. 2

EDITORIAL COMMITTEE

STEPHEN ALFRED FORBES WILLIAM TRELEASE

HENRY BALDWIN WARD

PUBLISHED UNDER THE
AUSPICES OF THE GRADUATE SCHOOL BY
THE UNIVERSITY OF ILLINOIS

TABLE OF CONTENTS

	PAGE
Introduction	7
Materials and Methods of Study	7
Acknowledgments	8
Experimental Data	9
Toxity of Cupric Chloride, Cadmium Chloride, Ferric Chloride, Colloidal Copper, and Distilled Water	35
The Efficiency of the Goldfish as a Test Animal	40
The Effect of Temperature upon the Resistance of the Goldfish	42
Toxicity and the Expression of Relative Toxicity	42
Is the Toxicity of a Substance Due to Osmotic Pressure	46
Theory of the Poisoning Effect of Toxic Substances	46
A Comparison of Curves Obtained by other Workers	52
Discussion of Data	54
Summary of Conclusions	66
Bibliography	69

INTRODUCTION

The need of uniformity of remedial agents has long been recognized among therapeutists and pharmacologists. When the physiological activity of an agent is associated with or dependent upon its chemical constitution which can be determined by analysis the problem becomes a simple one. On the other hand when either the chemical constitution can not be determined or the activity of the substance is dependent upon some other factor independent of its constitution the problem becomes more complex. This difficulty has been overcome with more or less success by certain physiological assay methods, the history of which it is not deemed necessary to present as Baker (1913) has given an excellent review of the literature up to that date. Of the methods employed at present the most favored is Fagge and Stevenson's (1866) frog method as proposed by Houghton (1898) or some modification of it. Others have been suggested:—the blood pressure method, the guinea-pig method introduced by Laborde (1884) and further worked out by Reed and Vanderkleed (1908), the cat method of Hatcher and Brody (1910), the cockscomb method of Haskell (1914), the goldfish method of Pittenger and Vanderkleed (1915), and other methods.

The purpose of this investigation was to test the validity of the Pittenger and Vanderkleed goldfish method or to work out a usable modification of it. The problem then involved the development of a method and technic by which drugs or remedial agents, not readily assayed chemically, could be assayed or standardized physiologically by means of goldfish. In order to use the goldfish as test animals they must meet the following requirements: 1. They must be relatively constant in their reactions or resistance to the drug or agent to be standardized or at least there must be a constant seasonal rhythm. 2. They should be capable of being standardized with some standard of a conveniently assayable substance if seasonal rhythm is present. 3. They must be relatively sensitive to small variations in the concentration of the substance to be tested.

MATERIALS AND METHODS OF STUDY

A series of experiments was run with the goldfish to determine how far they would comply with the three requirements just mentioned. In order to do this the goldfish were tested with a number of substances varying in toxic activities. A number of solutions of each substance tested were prepared of which the concentration of each differed only 10% or less from that of the one next to it in the series. Two goldfish of known weights were then placed in two liters of each of the solutions contained in a three liter wide-mouth bottle. The survival time of each fish in each solution was noted and recorded. The bottles were kept stoppered when volatile substances

were being tested. The stock of fish was kept at as nearly constant temperature as possible by the addition of hot water to the aerated tap-water. The experiments were run at the same temperature as that of the stock by placing the experimental bottles in the stock tank. This eliminated any ill effect due to the sudden change of temperature (Wells 1914). By these experiments it was hoped to determine two things: (1) the fitness of the goldfish as a test animal and (2) the most adaptable range of survival time of the goldfish for pharmacodynamic assay work.

The goldfish used in these experiments were *Carassius carassius* L. (Meek and Hilderbrand 1910), the Crucian carp or goldfish. This is the goldfish commonly sold for aquaria. *C. auratus* is less common and was not obtainable for this work.

ACKNOWLEDGMENTS

The author desires to acknowledge his indebtedness to Dr. J. H. Beal, Director of Pharmaceutical Research, who suggested the following research and supplied the necessary funds for its conduct, as well as many helpful suggestions throughout the course of the work.

The author also extends his thanks to Dr. Victor E. Shelford, in whose laboratory the experiments were made, for much valuable advice and assistance and to Dr. C. H. Sisam for suggestions on mathematical points, for the application of which, however, the author assumes sole responsibility. The author's thanks are also due to Drs. Geo. D. Beal, H. B. Lewis, T. R. Ball, and H. E. Eastlack for frequent help in chemical problems.

EXPERIMENTAL DATA

In the study of the goldfish as a test animal it was deemed advisable to determine the uniformity or lack of uniformity of the resistance or susceptibility of the goldfish first to certain of the less toxic simple substances; then later to take up a study of the more toxic and the more complex substances. First the chlorides and nitrates of the alkali and alkaline earth metals were employed. Later the heavier metals, cupric chloride, cadmium chloride, and ferric chloride, and finally hydrochloric acid, potassium cyanide, methyl, ethyl, and isobutyl alcohols, phenol, caffeine, and pyridine were used. It was found that all substances tested, with the exception of $CuCl_2$, $CdCl_2$, and to a certain extent $FeCl_3$, have certain points in common when the toxic activity of varying amounts of the substance tested is considered. This can be best illustrated by a detailed study of one or two representative substances and by comparing these with the other substances employed. The experiments with lithium chloride will first be considered.

In the lithium chloride experiments the resistance of the goldfish to concentrations varying from 0.089 N. to 0.466 N. was tested. By referring to Table I it will be found that the goldfish died fairly uniformly in any given concentration of the lithium chloride solution. For other chlorides and nitrates see Tables II to XV. The 2.5 g. goldfish (Table III) having a survival time of 135 minutes and marked with an asterisk (*) was taken out of the sodium chloride solution foı dead, but when placed in an HCl solution

TABLE I

LITHIUM CHLORIDE. TEMPERATURE 21° C. DECEMBER 1, 1916

Normal	Weight of fish in grams	Survival time of fish in minutes	Normal	Weight of fish in grams	Survival time of fish in minutes	Remarks
0.466	2.8	36	0.200†	2.8	141	Daggers (†) indicate the range in which the greatest difference in survival times occured in any two solutions with the least difference in concentrations in which the fish died uniformly.
"	3.2	41	"	3.05	179	
0.388	3.0	46	0.166	2.8	234	
"	4.2	44	"	3.6	310	
0.322†	2.9	54	0.133	2.9	525	
"	3.2	58	"	3.4	925	
0.266†	2.9	92	0.111	3.0	1204	
"	3.2	96	"	3.2	1214	
0.222†	3.3	116	0.089	2.7	±1320	
"	3.35	112	"	3.0	1620	

showed very slight signs of life. All goldfish when taken out of a solution for dead were tested by placing them in a hydrochloric acid solution and if any signs of life were evidenced the goldfish was designated by an asterisk in experimental data as not dead. No corrections have been made either in this or subsequent tables or graphs since it was deemed as being within experimental error as well as within individual variation of the goldfish. For further discussion of the uniformity of the survival time of the goldfish see page 40. By a close examination of data of killing goldfish in different concentrations of lithium chloride (Table I) it is found that the survival time of

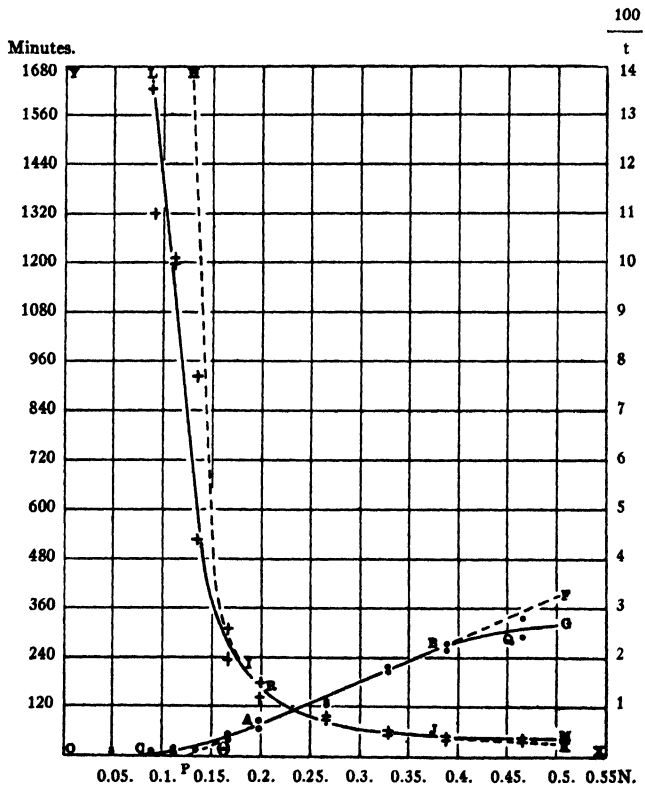


Figure 1. Lithium chloride. LIJM is the survival time curve. The survival time of the goldfish is plotted as ordinate and the concentration of the LiCl as abscissa. The crosses (+) are located from actual experimental data. CABG is the velocity of fatality curve. The concentration of the LiCl is plotted as abscissa and the reciprocal of the survival time in minutes or the velocity of fatality is plotted as ordinate. Instead of 1 over the survival time which gives the reciprocals, 100 over the survival time is used to avoid the use of fractions. The circles (●) are located by calculations from actual experimental data. The numbers at the left hand of the graphs represent minutes of survival time and those at right hand side of graphs represent units of velocity of fatality. The line PABF is the theoretical velocity of fatality curve and is a straight line. HIJK is the theoretical survival time curve.

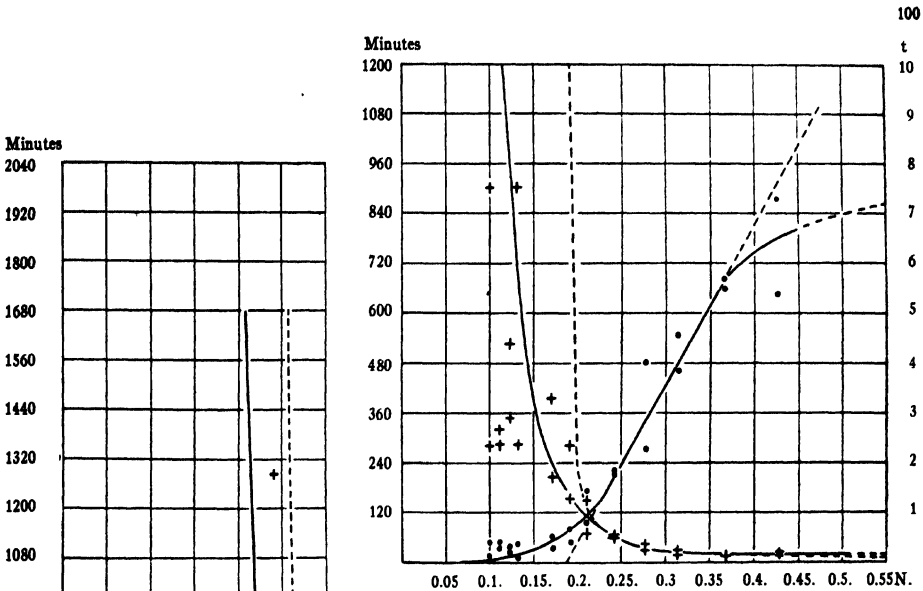


Figure 3. Potassium chloride

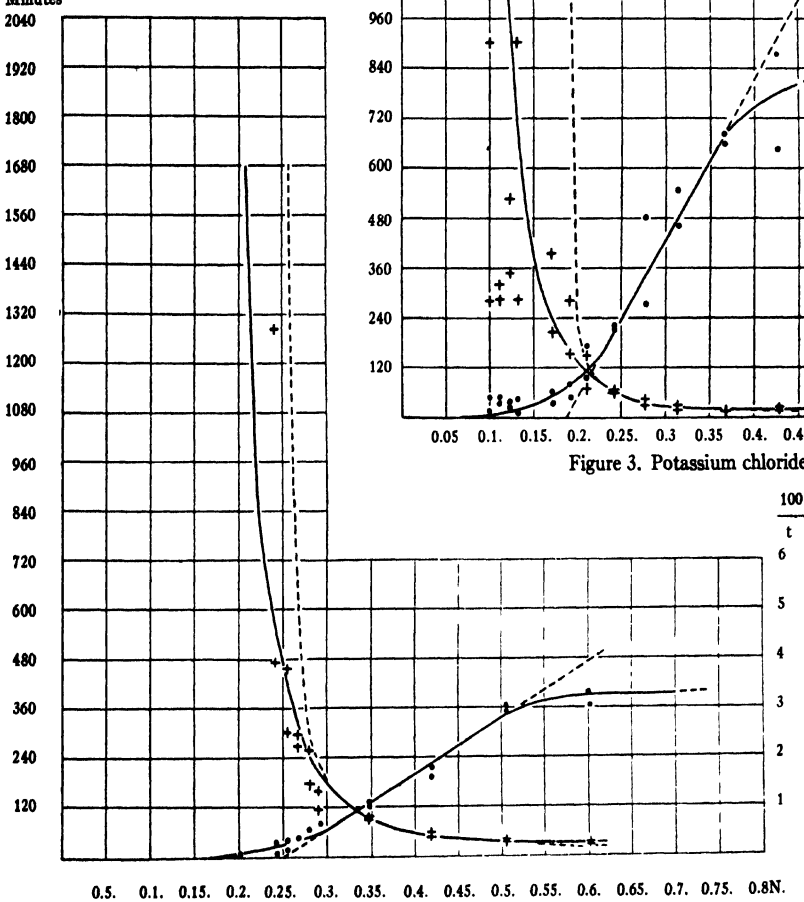


Figure 2. Sodium chloride

the goldfish does not increase in the same ratio as the concentration of the lithium chloride decreases, i. e., the survival time of the the goldfish is not in inverse proportion to the concentration of the lithium chloride employed. At higher concentrations (0.466, 0.388, and 0.322 N.) the increase in survival time of the goldfish was less rapid than the decrease in concentration of the solution. With concentrations from 0.322 to 0.133 N. there was a more rapid increase in survival time of the goldfish in proportion to the decrease in concentration of the solutions. And finally with concen-

trations from 0.133 to 0.089 N. there was again a less rapid increase in survival time in proportion to the decrease in concentration of the lithium chloride solutions. These points can be better illustrated by the graphic method, (Fig. 1). Let one block abscissa represent 0.05 N. LiCl and one block ordinate represent 120 minute survival time of the goldfish and plot data as represented in Table I. When the points (+) have been located on the graphs the curve LIJM can be drawn by interpolation. The crosses of this and all subsequent graphs are located from actual experimental data. The curve LIJM thus

TABLE II

SODIUM CHLORIDE. TEMPERATURE 21.5° C. NOVEMBER 19 TO 20, 1916

Normal	Weight of fish in grams	Survival time of fish in minutes	Normal	Weight of fish in grams	Survival time of fish in minutes	Remarks
0.600	2.5	28	0 277†	2.6	±178	
"	2.7	30	"	2.7	260	Daggers (†) as in Table
0.500†	2.7	33	0.266	2.6	±270	I. Fish were all alive
"	2.7	34	"	2.7	296	in 0.18, 0.15 and 0.124
0.417†	2.85	61	0.253	2.7	457	N. solutions after 10200
"	2.9	55	"	2.8	304	minutes when experi-
0.347†	2.6	97	0.241	2.65	478	ments were discon-
"	2.7	93	"	2.7	1290	tinued.
0.289†	2.75	114	0.201	?	2040	
"	2.8	155	"	3.0	9240	

TABLE III

SODIUM CHLORIDE. TEMPERATURE 21.5° C. APRIL 10, 1917

Normal	Weight of fish in grams	Survival time of fish in minutes	Normal	Weight of fish in grams	Survival time of fish in minutes	Remarks
0.600	2.7	35	0.278†	3.3	134	
"	3.8	38	"	3.4	129	
0.500†	2.5	35	0.263	2.4	130	
"	2.9	37	"	2.5	141	Daggers (†) as in Table
0.417†	2.5	40	0.253	2.4	255	I. *Fish was not dead
"	3.2	42	"	2.5	135*	when taken out of solu-
0.347†	2.3	56	0.241	2.5	295	tion.
"	2.5	68	"	2.9	400	
0.289†	2.7	115	0.200	2.4	±1020	
"	2.9	125	"	3.0	±1020	

TABLE IV

POTASSIUM CHLORIDE. TEMPERATURE 20.5° C. NOVEMBER 17, 1916

Normal	Weight of fish in grams	Survival time of fish in minutes	Normal	Weight of fish in grams	Survival time of fish in minutes	Remarks
0.434	2.9	14	0.192	2.85	151	
"	3.2	17	"	2.9	282	
0.378	2.9	11	0.172	3.0	207	
"	3.0	16	"	3.1	396	
0.328†	2.8	22	0.134	2.9	286	Daggers (†) as in Table I. *Fish was not dead when taken out of solution.
"	3.0	26	"	2.9	±900	
0.286†	3.2	25*	0.122	2.8	347	
"	3.3	44	"	3.1	527	
0.243†	2.9	55*	0.112	3.1	318	
"	2.8	57	"	3.2	292	
0.214†	2.9	69	0.102	3.55	279	
"	2.8	150	"	2.8	±900	

drawn resembles that of an hyperbola and has been designated as the survival time curve the nature of which can be better illustrated by drawing the reciprocal curve. In the reciprocal curve the reciprocal of the survival time of the goldfish is plotted as ordinate. The normality is plotted as in the survival time curve. To avoid the use of fractions 100 over the survival time is taken as the reciprocal. One block ordinate represents one unit reciprocal. The circles (●) represent the location of the reciprocals. The curve CABG is drawn by interpolation and has been designated as the velocity of fatality curve. By an examination of this curve it is seen that it rises very slowly from the point C to A, i.e., in low concentrations, more rapidly from A to B, i.e., in higher concentrations, and again there is a falling off from B to G at still higher concentrations. By a closer examination of the curve it is seen that the portion from A to B approaches a straight line and for all practical purposes this portion can be considered as such. The point C where this curve cuts the X-axis has been designated as the actual threshold of toxicity concentration, i.e., the concentration below which the substance will not kill the goldfish. The portion of the curve from A to B is not a straight line but approaches a straight line in that the direction of curvature is being reversed from that of the curvature from C to A to that of the curvature from B to G (See velocity of fatality curves, Figures 1 to 21.) For a further discussion of the velocity of fatality curve see pages 48, 52. The portion from A to B of the curve CABG if considered as a straight line and prolonged cuts the X-axis at the point P. The curve PABF thus drawn has been designated as the theoretical velocity of fatality curve and the point P has been designated as the theoretical threshold of toxicity

concentration. The curve HIJK is an equilateral hyperbola drawn from calculations and has been designated as the theoretical survival time curve. The two curves HIJK and LIJM show the variation of the actual survival

TABLE V

AMMONIUM CHLORIDE. TEMPERATURE 21° C. NOVEMBER 24 TO 25, 1916

Normal	Weight of fish in grams	Survival time of fish in minutes	Normal	Weight of fish in grams	Survival time of fish in minutes	Remarks
0.352	3.5	29	0.141	3.25	357	
"	3.7	20	"	3.4	±600	
0.319	3.6	30	0.115	3.15	320	
"	3.8	31	"	3.9	297	
0.268†	3.45	38	0.096	3.2	547	
"	4.0	37	"	3.2	±1020	Daggers (†) as in Table
0.249†	2.8	48	0.064	3.1	±1020	I.
"	3.2	64	"	3.3	±1020	
0.224†	2.5	99	0.032	3.1	376	
"	3.7	90	"	3.4	1080	
0.166	2.9	283				
"	3.2	285				

TABLE VI

AMMONIUM CHLORIDE. TEMPERATURE 21.5° C. APRIL 12, 1917

Normal	Weight of fish in grams	Survival time of fish in minutes	Normal	Weight of fish in grams	Survival time of fish in minutes	Remarks
0.351	2.1	17	0.160	2.8	166	
"	4.3	28*	"	3.7	261	
0.320	2.8	26	0.141	2.3	111	Daggers (†) as in Table
"	3.0	22	"	?		I. *Fish was not dead
0.268†	3.0	48	0.115	3.0	376	when taken out of solu-
"	3.2	40	"	3.5	106	tion.
0.257†	2.7	51	0.096	2.7	123	** Fish was alive after
"	2.9	43	"	2.7	663	5040 minutes when
0.224†	2.8	53	0.064	2.5	±1080	experiment was discon-
"	2.8	65	"	2.8	±1080	tinued.
0.186	2.5	141	0.041	2.5	±1080*	
"	2.8	95	"	?	——**	

time curve from that of an equilateral hyperbola. To summarize: in the lithium chloride and all toxic substances tested with the exception of $CuCl_2$, $CdCl_2$, and to a certain extent $FeCl_3$ the following conditions were met:— 1. A concentration (the point C, about 0.073 N. LiCl), the threshold of toxicity concentration, was found below which the goldfish were not killed. 2. Just above the threshold of toxicity concentration the rate of fatality, as expressed by the reciprocal of the survival time, increased very slowly with increase in concentration of the toxic substance employed. This is represented by the portion C to A, about 0.073 to 0.19 N. LiCl, of the velocity of fatality curve CABG (Fig. 1). 3. With higher concentrations, concentrations

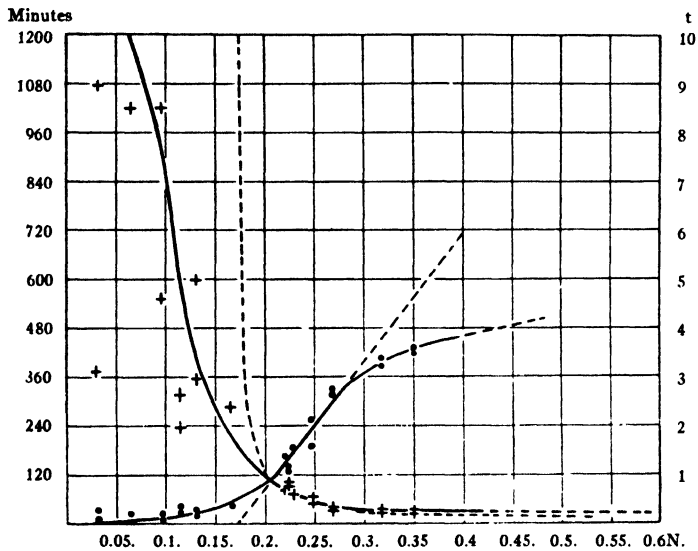


Figure 4. Ammonium chloride

sufficient to kill the goldfish in not less than 54 to 58 minutes and not more than 234 to 310 minutes in lithium chloride solutions, the velocity of fatality increased more rapidly in proportion to the increase in concentration of the toxic substance, and this portion of the velocity of fatality curve approaches a straight line. (The portion A to B, curve CABG, Fig. 1.) Table XXIV shows minimum and maximum survival time of goldfish and concentration of toxic substances tested where its velocity of fatality curve approaches a straight line. The daggers (†) in Tables I to XXIII also indicate the concentrations of the substances and the survival time of the goldfish where their velocity of fatality curves approach a straight line. 4. At still higher concentrations (0.375 to 0.45 N. LiCl) the increase in the velocity of fatality was again less rapid in proportion to the increase in concentration of the

TABLE VII

SODIUM NITRATE. TEMPERATURE 21° C. DECEMBER 9, 1916

Normal	Weight of fish in grams	Survival time of fish in minutes	Normal	Weight of fish in grams	Survival time of fish in minutes	Remarks
0.500	2.7	61	0.260†	3.0	134	Daggers (†) as in Table I.
"	2.9	164	"	3.4	274	
0.460	2.7	116	0.220†	2.6	171*	*Fish was not dead when taken out of solution.
"	2.7	118	"	2.7	196	
0.440	2.65	148	0.180	2.6	433	
"	3.2	68	"	3.0	656	Fish in 0.12 N. and 0.10 N. solutions were alive after 1680 minutes when experiments were discontinued.
0.380†	2.9	122*	0.150	2.5	593*	
"	3.1	109	"	2.9	±840	
0.310†	3.05	133				
"	3.4	180				

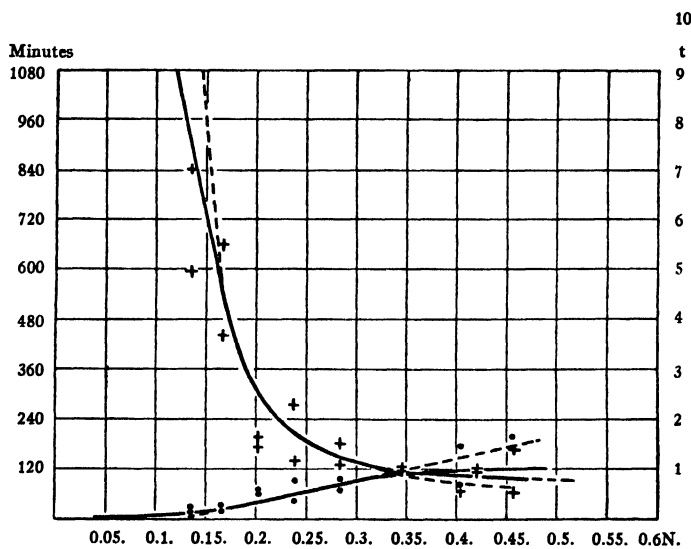


Figure 5. Sodium nitrate

solution. See the portion B to Q (Fig. 1). 5. At the highest concentrations tested the velocity of fatality curve a second time approaches a straight line but with a less rapid increase of velocity of fatality in proportion to the concentration of the solution than the portion of the velocity of fatality curve represented by the portion A to B, curve CABG (Fig. 1). (The portion Q to G,

Fig. 1.) This last point is better illustrated by the curves represented in Figures 2 to 20. These curves are logarithmic in nature. See pages 48, 51 for discussion of the theoretical equation for the velocity of fatality curve.

TABLE VIII

AMMONIUM NITRATE. TEMPERATURE 21° C. DECEMBER 18, 1916

Normal	Weight of fish in grams	Survival time of fish in minutes	Normal	Weight of fish in grams	Survival time of fish in minutes	Remarks
						Daggers (†) as in Table I.
0.309	1.95	29*	0.120	2.0	±720	*Fish was not dead when taken out of solution.
"	2.4	32	"	2.3	±2160	
0.253†	2.3	37	0.100	2.3	±1080	
"	2.7	52	"	2.4	±1800	*[1]A close approximate survival time.
0.213†	2.4	78	0.080	1.7	1620	
"	2.4	82*	"	1.9	1800	*[2] Fish was alive after 4 days when taken out of solution and experiment discontinued.
0.173	2.1	228*[1]	0.066	1.7	5625	
"	2.5	228*[1]	"	1.7	——*[2]	
0.140	2.3	371	0.053	2.2	5400*[1]	
"	?	404	"	2.0	——*[2]	Fish were alive after 4 days in 0.033 N. Solution when experiment was discontinued.

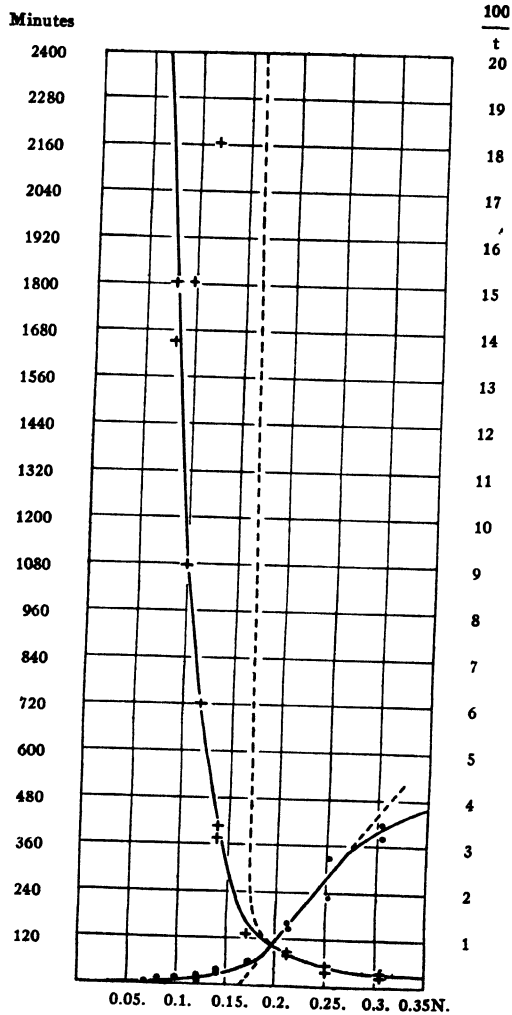


Figure 6. Ammonium nitrate

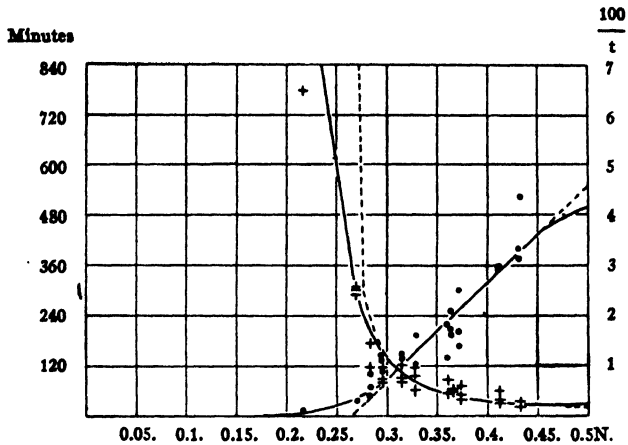


Figure 7. Magnesium chloride

TABLE IX

MAGNESIUM CHLORIDE. TEMPERATURE 20.5°C. NOVEMBER 8 TO 14, 1916

Normal	Weight of fish in grams	Survival time of fish in minutes	Normal	Weight of fish in grams	Survival time of fish in minutes	Remarks
2.158	4.4	10.5				
0.432†	3.3	23	0.298	3.2	82	
"	4.1	34	"	3.4	91	
"	5.0	30*	"	3.6	86	
0.411†	4.2	33	0.283	3.6	117	
"	5.4	35	"	5.1	174	
"	6.2	58	"	6.3	270	Daggers (†) as in Table I.
0.373†	3.4	40	0.270	3.7	183	
"	3.7	45	"	5.5	132	*Fish was not dead when taken out of solution.
"	5.8	70	"	6.0	239	
0.360†	3.9	42	0.257	3.3	306	
"	5.7	57	"	3.7	291	
"	6.1	61	"	4.3	301	
0.328†	3.4	62	0.216	5.4	780	
"	3.9	118				
"	7.6	99	"	4.3	1200	
0.313†	4.2	121	0.142	?	30420	
"	5.0	88	"	?	15180	
"	5.5	80	"	?	4680	

TABLE X

CALCIUM CHLORIDE. TEMPERATURE 21°C. NOVEMBER 21 AND DECEMBER 2, 1916

Normal	Weight of fish in grams	Survival time of fish in minutes	Normal	Weight of fish in grams	Survival time of fish in minutes	Remarks
0.583	2.6	43	0.213	2.3	136	
"	2.6	43	"	2.5	±900	
0.356†	1.9	48*	0.202	?	±1080	
"	2.05	59	"	3.1	±1920	Daggers (†) as in Table I.
0.347†	2.6	57*	0.171	2.3	2640	
"	2.7	66*	"	2.5	4080	*Fish was not dead when taken out of solution.
0.299	2.0	65	0.168	2.8	6627	
"	2.2	90	"	3.1	±2760	
0.290†	2.8	91	0.142	2.5	1391	*[1]Experiment discontinued after 4320 minutes. Fish were all alive.
"	3.0	139	"	3.0	4331	
0.250†	2.7	182	0.140	2.9	1920	
"	2.9	111	"	3.4	4320	
0.249†	2.3	174	0.128	—	*[1]	
"	2.25	190	"	—	*[1]	

TABLE XI

STRONTIUM CHLORIDE. TEMPERATURE 20°C. NOVEMBER 25, 1916

Normal	Weight of fish in grams	Survival time of fish in minutes	Normal	Weight of fish in grams	Survival time of fish in minutes	Remarks
0.458	3.4	50	0.289†	3.3	80	
"	2.6	59	"	4.1	88	
0.380	2.8	46	0.237†	3.6	168	Daggers (†) as in Table I.
"	3.75	51	"	3.6	347	
0.318†	3.4	59	0.193	2.7	±1020	
"	3.5	76	"	3.4	±1860	

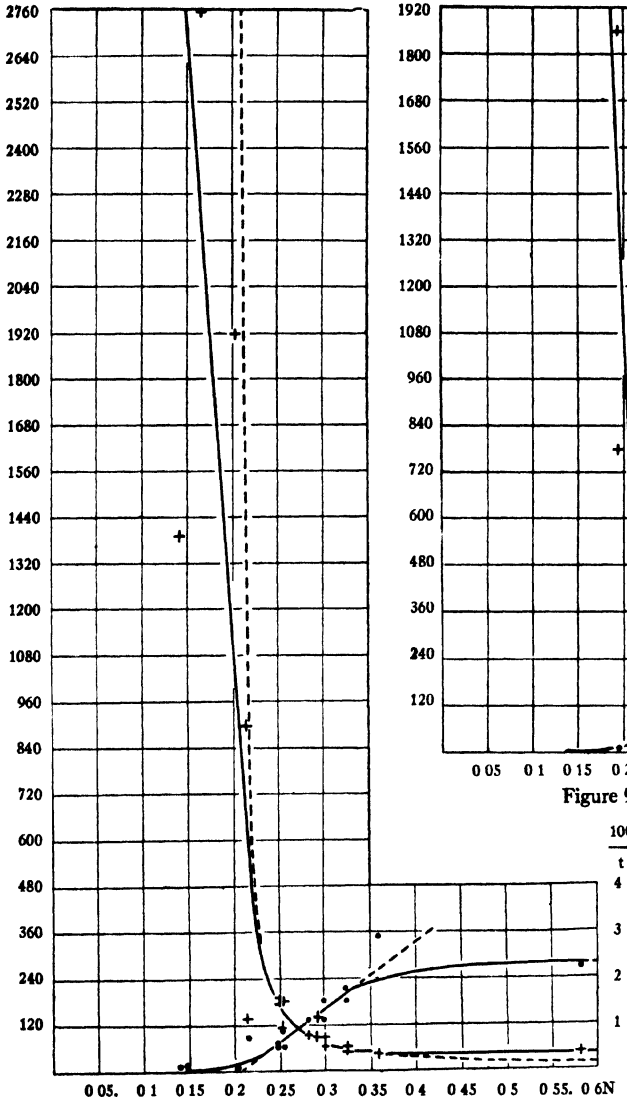


Figure 8. Calcium chloride

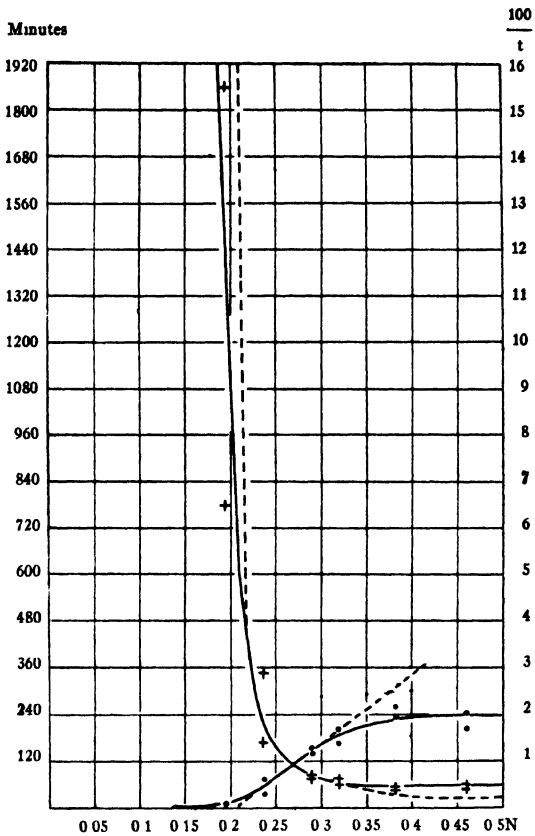


Figure 9 Strontium chloride

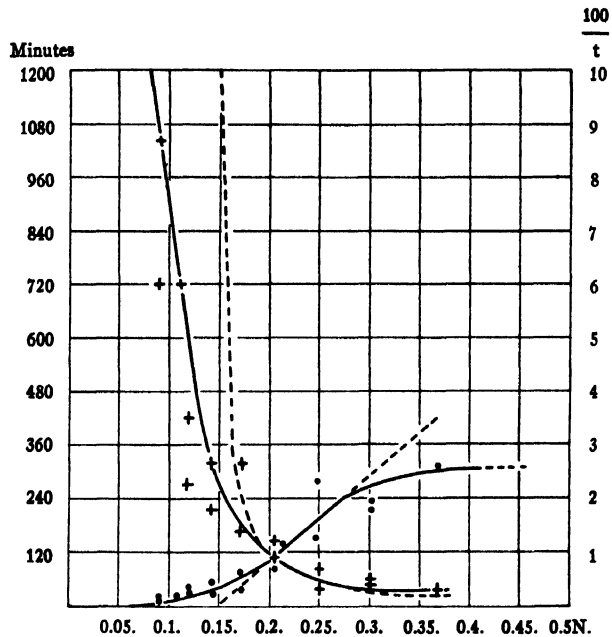


Figure 10. Barium chloride

TABLE XII

BARIUM CHLORIDE. TEMPERATURE 20.5°C. NOVEMBER 22, 1916

Normal	Weight of fish in grams	Survival time of fish in minutes	Normal	Weight of fish in grams	Survival time of fish in minutes	Remarks
0.368	3.0	38	0.143	3.35	216	
"	3.2	38	"	3.7	314	
0.302	3.2	51*	0.119	3.3	±420	Daggers (†) as in Table I.
"	3.2	56	"	3.7	±272	
0.249†	3.5	43	0.107	3.5	±720	*Fish was not dead when taken out of solution.
"	3.5	80	"	3.6	±720	
0.208†	3.35	113	0.090	3.2	±720	
"	3.5	144	"	3.8	1020	
0.172†	2.8	169				
"	3.7	316				

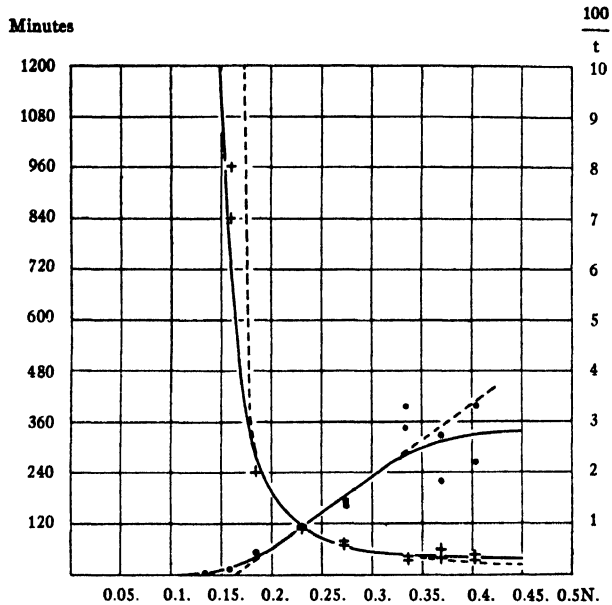


Figure 12. Magnesium nitrate

TABLE XIII

MAGNESIUM NITRATE. TEMPERATURE 21°C. DECEMBER 15 AND 16, 1916

Normal	Weight of fish in grams	Survival time of fish in minutes	Normal	Weight of fish in grams	Survival time of fish in minutes	Remarks
						Daggers (†) as in Table 1.
0.405	2.7	33*	0.229†	2.2	107*	*Fish was not dead when taken out of solution.
"	2.7	46*[1]	"	2.9	104*	
0.370†	2.6	37*	0.185	2.4	±240	
"	2.7	56*	"	2.6	±240	*[1]Fish had been dead possibly a few minutes. Fish were alive in 0.132 N. 0.106 N. 0.088 N. and 0.07 N. solutions after 3120 minutes when experiments were terminated.
0.334†	2.4	33*	0.158	1.9	±840	
"	2.5	35*	"	2.5	±960	
0.273†	2.9	70*				
"	3.4	73*				

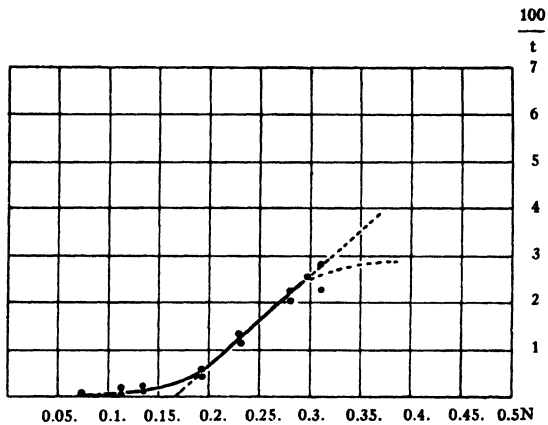


Figure 13. Calcium nitrate

TABLE XIV

CALCIUM NITRATE. TEMPERATURE 21°C. DECEMBER 16, 1916

Normal	Weight of fish in grams	Survival time of fish in minutes	Normal	Weight of fish in grams	Survival time of fish in minutes	Remarks
0.311	2.6	42	0.133	2.0	±840	
"	3.0	44	"	2.1	±840	
0.281†	2.2	45	0.111	2.4	±1200	
"	2.4	50	"	2.4	±1200	Daggers (†) as in Table I.
0.229†	2.4	75	0.088	2.4	2116	
"	2.4	85	"	2.2	4936	
0.192†	2.6	186	0.074	2.5	2580	
"	2.6	186	"	2.0	2920	

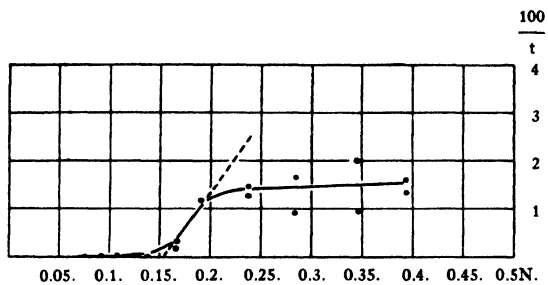


Figure 14. Strontium nitrate

TABLE XV

STRONTIUM NITRATE. TEMPERATURE 21°C. DECEMBER 14, 1916

Normal	Weight of fish in grams	Survival time of fish in minutes	Normal	Weight of fish in grams	Survival time of fish in minutes	Remarks
0.394	2.7	63	0.165†	3.5	±300	
"	2.5	75	"	3.5	600	
0.347	2.7	108	0.137	2.9	435	Daggers (†) as in
"	2.9	50	"	3.4	±990	Table I.
0.283	3.0	60	0.110	2.2	816	Fish were alive in
"	3.2	111	"	3.5	6240	0.073 N. solution after
0.238	3.0	70	0.091	3.2	1923	5760 minutes when ex-
"	2.8	85	"	2.8	8760	periment was termin-
0.192†	3.0	92				ated.
"	3.2	87				

TABLE XVI

POTASSIUM CYANIDE. TEMPERATURE 21.5° C.

Normal	Weight of fish in grams	Survival time of fish in minutes	Normal	Weight of fish in grams	Survival time of fish in minutes
0.2×10^{-1}	2.9	35*	0.5×10^{-4}	2.7	118
"	4.5	59	"	3.0	94
0.12×10^{-1}	3.1	61	0.375×10^{-4}	3.0	138
"	3.4	96	$0.25\dagger\times10^{-4}$	3.1	146*
0.6×10^{-2}	3.7	96	"	3.5	204
"	4.3	64	$0.235\dagger$		
			$\times10^{-4}$	2.9	192
0.375×10^{-2}	3.3	67	"	3.6	163
"	3.3	68	$0.22\dagger\times10^{-4}$	2.3	128
0.2×10^{-2}	2.8	69	"	4.2	179
"	4.1	97	$0.217\dagger$		
			$\times10^{-4}$	2.5	138*
0.1×10^{-2}	3.6	43*	"	3.7	253
"	4.3	71	$0.215\dagger$		
			$\times10^{-4}$	3.8	296
0.5×10^{-3}	3.4	123	"	3.8	1658
"	3.7	90	$0.211\dagger$		
			$\times10^{-4}$	2.8	178
0.25×10^{-3}	3.4	98	"	3.9	928
"	4.2	98	$0.205\dagger$		
			$\times10^{-4}$	2.9	2135
0.162×10^{-3}	2.7	84	"	3.8	1945
"	3.0	84	0.195×10^{-4}	2.8	505
0.135×10^{-3}	3.2	84	"	3.2	2785
"	3.5	84	0.185×10^{-4}	3.1	715
0.1×10^{-3}	3.3	70*	"	4.2	655
"	3.6	67*	0.175×10^{-4}	2.4	1519
0.85×10^{-4}	2.9	79	"	4.2	$\pm$1020
"	2.95	79	0.12×10^{-4}	2.9	2615
0.7×10^{-4}	2.6	82	"	3.0	7080
"	2.9	74*			

Daggers (†) as in Table I

*Fish was not dead when taken out of solution

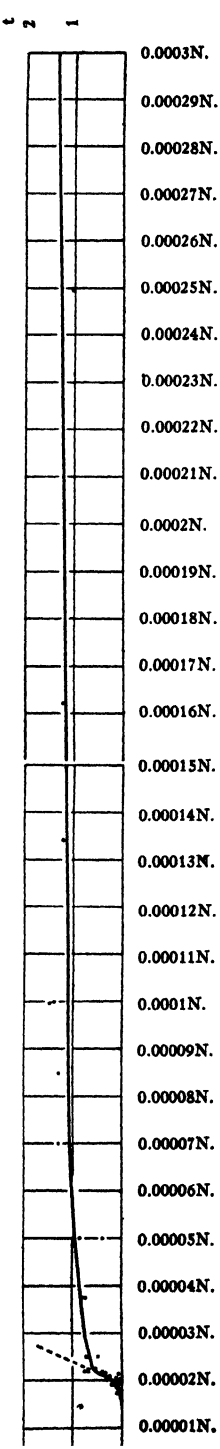


Fig. 14 (at right). Potassium cyanide. Velocity of fatality curve only

TABLE XVII

HYDROCHLORIC ACID. TEMPERATURE 21.5° C.

Normal	Weight of fish in grams	Survival time of fish in minutes	Normal	Weight of fish in grams	Survival time of fish in minutes
8.89×10^{-3}	2.8	27*	$0.31\dagger\times10^{-3}$	3.2	353
"	3.4	34	"	4.0	246
7.32×10^{-3}	3.0	22*	0.209×10^{-3}	4.5	±1000
"	5.7	33*	"	5.5	±1000
4.19×10^{-3}	2.8	30	0.125×10^{-3}	3.4	±1200
"	5.0	36	"	4.0	±2520
2.09×10^{-3}	3.0	37	8.37×10^{-5}	3.5	±1200
"	5.1	40	"	5.0	±2520
1.05×10^{-3}	3.0	50*	6.27×10^{-5}	5.0	±1200
"	5.8	70	"	4.8	660
$0.9\dagger\times10^{-3}$	3.2	46*	4.18×10^{-5}	4.7	±1200
"	4.0	72*	"	4.1	697
$0.774\dagger\times10^{-3}$	2.2	78*	3.13×10^{-5}	5.1	±1200
"	3.3	87	"	5.2	±2420
$0.627\dagger\times10^{-3}$	4.7	98	2.09×10^{-5}	3.3	553*
"	4.3	110	"	4.1	±1200
$0.523\dagger\times10^{-3}$	3.9	134	1.57×10^{-5}	5.7	584
"	4.1	161	"	3.9	794
$0.418\dagger\times10^{-3}$	4.2	339			
"	5.2	480*			

Daggers (†) as in Table I

*Fish was not dead when taken out of solution

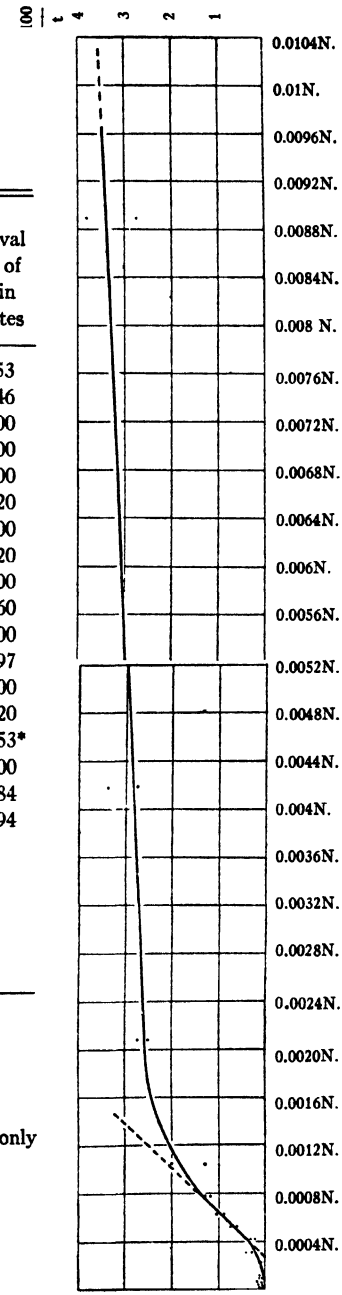


Fig. 15 (at right). Hydrochloric acid. Velocity of fatality curve only

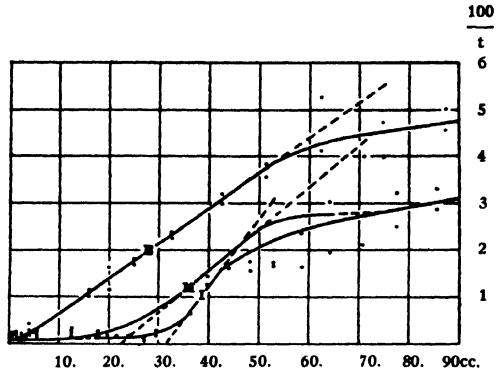


Figure 16. Methyl alcohol (M); Ethyl alcohol (E); Iso-butyl alcohol (I). Velocity of fatality curves only.

TABLE XVIII

METHYL ALCOHOL. TEMPERATURE 21.5° C.

cc. per l.	Weight of fish in grams	Survival time of fish in minutes	cc. per l.	Weight of fish in grams	Survival time of fish in minutes	Remarks
62.5	2.3	36*	6.0	2.8	603	
"	3.4	38*	"	4.0	258	
52.5	2.3	40*	4.0	3.6	517	
"	3.2	45	"	4.2	502	
42.5†	2.0	52	2.5	2.4	245	
"	3.6	57*	"	2.5	534	Daggers (†) as in Table I.
32.5†	3.6	±109	1.5	3.2	651	
"	4.2	±109	"	3.4	906	*Fish was not dead when taken out of solution.
25.0	3.0	206	1.0	2.9	507	
"	4.2	32	"	3.8	±906	
20.0	3.4	271	0.5	3.7	581	
"	3.4	421	"	5.0	901	
16.0	2.8	151	0.25	2.4	791	
"	3.8	299	"	3.2	646	
12.5	3.0	163				
"	2.4	325				

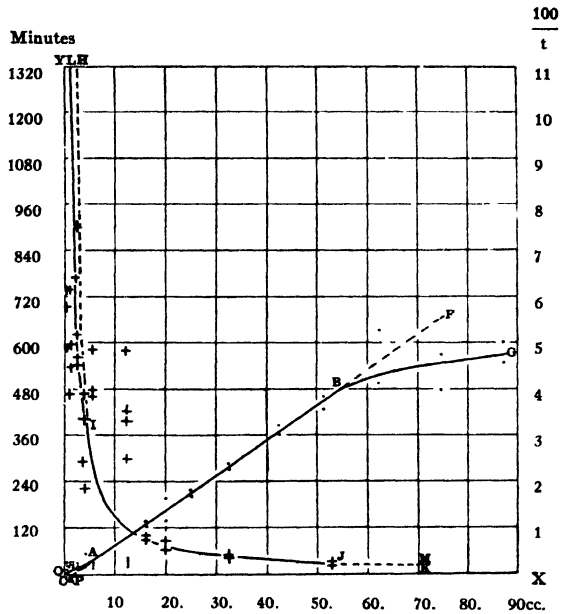


Figure 17. Ethyl alcohol

TABLE XIX

ETHYL ALCOHOL. TEMPERATURE 21.5° C.

cc. per l.	Weight of fish in grams	Survival time in minutes	cc. per l.	Weight of fish in grams	Survival time in minutes	Remarks
87.5	2.7	20	6.0	3.2	480	
"	3.3	22	"	3.3	475	
75.0	3.1	21*	"	2.6	462	
"	3.3	25	"	4.1	582	
62.5	3.0	19*	4.0	3.0	469	
"	3.3	24	"	4.5	403	
51.5†	2.8	26*	"	2.9	222	
"	3.5	28	"	3.0	290	Daggers (†) as in Table I.
42.5†	3.5	31	2.5	3.5	±900	
"	3.9	33*	"	4.0	±900	*Fish was not dead when taken out of solution.
32.5†	3.3	42	"	3.2	±540	
"	3.5	44*	"	5.0	620	
25.0†	2.8	56	"	3.4	561	
"	4.0	59*	"	5.0	771	
20.0†	2.5	61	1.5	2.8	593	
"	3.9	85	"	3.4	538	
16.0†	3.2	88*	1.0	2.4	738	
"	2.5	98*	"	2.5	465	
12.5	3.6	299	0.5	2.4	738	
"	4.3	579	"	3.3	583	
"	2.2	397	0.25	3.0	396	
"	3.4	472	"	3.0	694	

TABLE XX

ISO-BUTYL ALCOHOL. TEMPERATURE 21.5°C.

cc. per l.	Weight of fish in grams	Survival time of fish in minutes	cc. per l.	Weight of fish in gram	Survival time of fish in minutes	Remarks
14.	3.2	20	6.0	2.6	43*	Boiling point 102° to 104° C.
"	3.4	25	"	2.8	14*	
12.5	2.9	24	5.0	3.3	64	
"	3.2	30	"	3.9	78*	Daggers (†) as in Table I.
11.0	2.9	28*	4.0	2.8	101*	
"	3.2	32	"	5.5	130*	*Fish was not dead when taken out of solution.
9.0	2.9	33	3.25	3.3	464	
"	3.5	36*	"	3.4	654	
7.5	2.9	41*	2.5	2.8	1680	
"	5.5	46	"	4.2	900	
20.0	3.0	17	4.4	3.0	57*	Boiling point 104° to 105° C.
"	4.0	18	"	4.9	63*	
16.0	2.4	23	4.0	3.8	70	
"	3.3	29	"	3.9	80*	
12.5	3.0	29	"	3.6	70*	
"	4.0	29	"	4.5	83	
9.0	3.4	35	3.62	2.3	157*	
"	4.2	39*	"	3.5	162	
8.55	4.2	30*	3.3	2.6	302	
"	4.5	35*	"	3.9	328*	
7.77	4.3	31	2.97	3.2	628	
"	4.4	40	"	5.0	302	
7.07	3.3	24	2.5	2.9	664	
"	5.9	48*	"	4.0	434	
6.42†	3.6	33*	1.5	3.0	270	
"	5.4	51*	"	3.9	509	
6.0†	3.3	46	1.0	2.8	1425	
"	4.5	43	"	4.0	±1140	
5.85†	3.5	61	0.5	2.3	510	
"	4.4	42*	"	2.9	665	
5.3	3.0	59	0.25	2.3	734	
"	4.3	61*	"	4.1	419	
4.85	2.5	58*				
"	5.4	66*				
9.0	2.8	40	1.5	3.1	389	Boiling point 105° to to 107° C.
"	3.3	40	"	4.7	703	
6.0	3.3	42	1.0	3.8	783	
"	3.3	42	"	4.5	663	
4.0	2.8	77	0.5	4.0	390	
"	3.7	±87	"	4.2	664	
2.52	3.1	282	0.25	3.8	784	
"	4.2	262*	"	4.0	±1200	

TABLE XXI

PHENOL. TEMPERATURE 21.5°C.

g. per liter	Weight of fish in grams	Survival time of fish in minutes	g. per liter	Weight of fish in grams	Survival time of fish in minutes	Remarks
3.45	3.2	9	0.345†	2.4	59	
"	3.7	9	"	2.6	103	
2.58	3.3	10	0.31†	2.9	81	
"	3.9	10	"	3.4	53	
1.72	2.4	13	0.26†	2.55	104	
"	3.1	13	"	2.8	132	
1.036	2.5	17	0.17	3.2	125	Daggers (†) as in Table
"	3.7	24	"	3.5	136	I.
0.69	2.8	18	0.10	3.2	91	
"	3.8	30	"	2.9	77	
0.517	2.3	32	0.07	3.3	292	
"	2.5	38	"	3.7	217	
0.414†	2.0	37	0.051	?	92	
"	3.4	51	"	3.4	140	

TABLE XXII

CAFFEINE. TEMPERATURE 17°C.

g. per liter	Weight of fish in grams	Survival time of fish in minutes	g. per liter	Weight of fish in grams	Survival time of fish in minutes	Remarks
2.22	2.4	13	0.32†	2.8	22	
"	2.9	10	"	3.5	83	
1.58	3.0	14	0.284†	3.4	94	
"	3.0	18	"	3.8	256	
0.95	3.0	22	0.19	2.4	319	
"	3.2	23	"	2.4	359	Daggers (†) as in Table
0.712	2.6	23	0.095	2.8	322	I.
"	2.9	25	"	3.0	1140	
0.47	2.8	23	0.047	2.8	1200	
"	3.0	50	"	3.1	1652	
0.40†	2.2	42	0.019	3.0	1320	
"	3.2	45	"	3.5	2760	

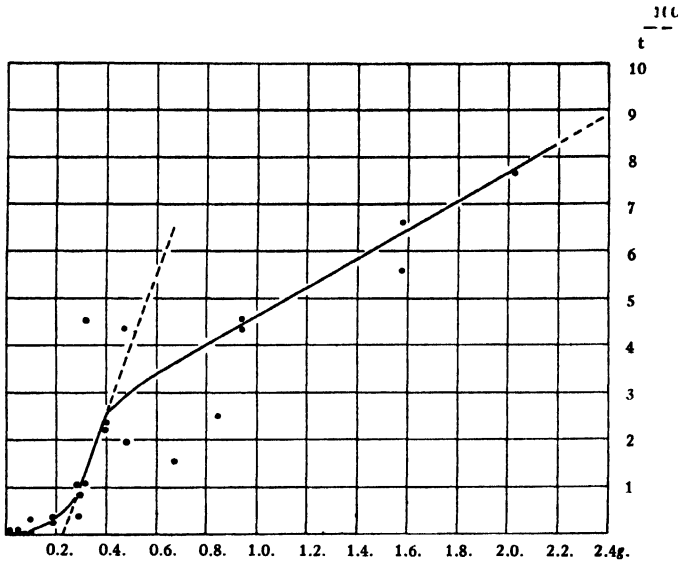


Figure 18. Caffeine. Velocity of fatality curve only. Abscissa represents g. per liter

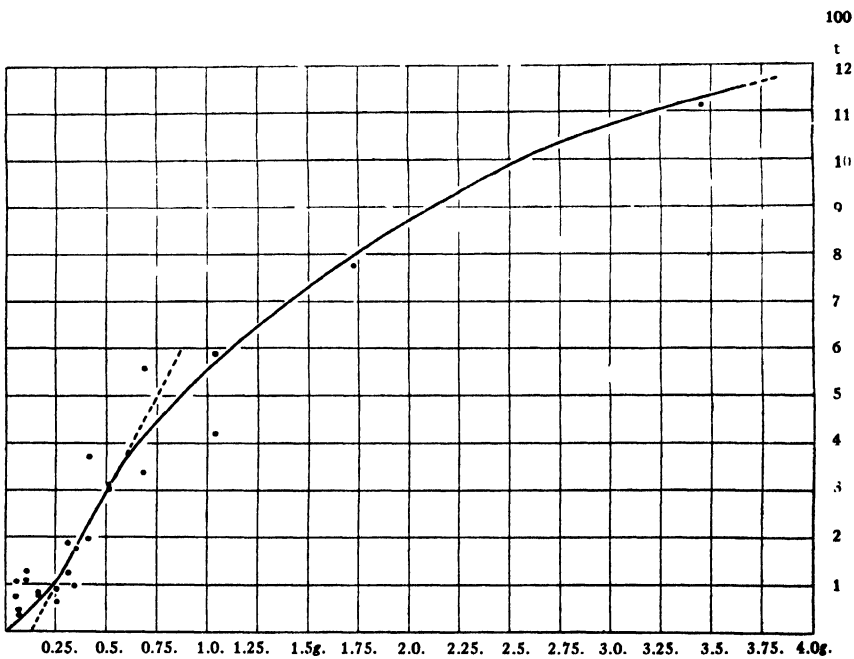


Figure 19. Phenol. Velocity of fatality curve only. Abscissa represents g. per liter.

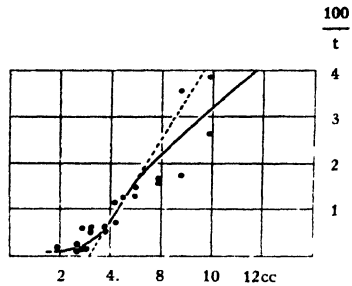


Figure 20. Pyridine. Velocity of fatality curve only. Abscissa represents cc. per liter

TABLE XXIII

PYRIDINE. TEMPERATURE 17.5°C.

cc. per liter	Weight of fish in grams	Survival time of fish in minutes	cc. per liter	Weight of fish in grams	Survival time of fish in minutes	Remarks
7.87	2.0	26*	3.0	2.7	±720	
"	2.6	38	"	3.1	±720	
6.75	2.4	28	2.81	3.5	180	
"	3.6	58	"	3.7	+900	
5.81	3.3	63	2.62	3.3	420	Daggers (†) as in Table I.
"	3.8	61	"	4.0	±1080	
4.87	2.1	68	1.87	2.4	715	*Fish was not dead when taken out of solution.
"	2.9	78	"	2.9	610	
4.5†	2.2	82	10.0*[1]	3.1	13*	*[1]Temperature 21.5 C. Fish were suffering with gas disease.
"	4.1	83	" *[1]	3.1	15*	
4.12†	2.5	87	5.0*[1]	2.2	40	
"	2.7	140	" *[1]	2.5	40	
3.75†	2.2	175	2.0*[1]	3.3	±1020	
"	3.1	187	" *[1]	3.3	660*	
3.19†	2.2	180				
"	2.2	190				

TABLE XXIV

The maximum and minimum concentration of substance and maximum and minimum survival time of goldfish within the range in which the velocity of fatality curve approaches a straight line.

Substance	Normal	Survival time of fish in minutes
NaCl	0.500	33
"	"	34
"	0.277	178
"	"	260
LiCl	0.322	54
"	"	58
"	0.166	234
"	"	310
KCl	0.328	22
"	"	26
"	0.214	69
"	"	150
NH_4Cl	0.168	38
"	"	37
"	0.224	99
"	"	90
$NaNO_3$	0.380	122
"	"	109
"	0.220	171
"	"	196
NH_4NO_3	0.253	37
"	"	52
"	0.213	78
"	"	82
$MgCl_2$	0.432	23
"	"	30
"	"	34
"	0.313	61
"	"	88
"	"	80
$CaCl_2$	0.356	48
"	"	59
"	0.249	174
"	"	190
$SrCl_2$	0.318	59
"	"	76
"	0.237	168
"	"	347
$BaCl_2$	0.249	43
"	"	80
"	0.172	169
"	"	316
$Mg(NO_3)_2$	0.370	37
"	"	56
"	0.229	107
"	"	104
$Ca(NO_3)_2$	0.281	45
"	"	50
"	0.192	186
"	"	186
$Sr(NO_3)_2$	0.192	92
"	"	87
"	0.165	300
"	"	600
KCN	0.25×10^{-4}	146
"	"	204
"	0.2×10^{-4}	2135
"	"	1945
HCl	8.99×10^{-4}	46
"	"	72
"	0.313×10^{-4}	1200
"	"	2520
g. per L.		
Phenol	0.414	37
"	"	51
"	0.259	104
"	"	132
Caffeine	0.396	42
"	"	45
"	0.285	256
"	"	94
cc. per L.		
Methyl Alcohol	42.5	52
"	"	58
"	25.0	206
"	"	326
Ethyl Alcohol	51.5	26
"	"	28
"	16.0	98
"	"	88
Iso-butyl Alcohol	6.42	33
"	"	51
"	5.85	61
"	"	42
Pyridine	4.5	82
"	"	83
"	3.187	180
"	"	190

TOXICITY OF CUPRIC CHLORIDE, CADMIUM CHLORIDE, FERRIC CHLORIDE, COLLOIDAL COPPER, AND DISTILLED WATER

It has already been pointed out that the toxic activity of various concentrations of $CuCl_2$, $CdCl_2$ and $FeCl_3$ did not follow the same general law as did all other substances tested. The toxicity of the $CuCl_2$ at very high concen-

TABLE XXV

CUPRIC CHLORIDE. TEMPERATURE 21°C.

Normal	Weight of fish in grams	Survival time of fish in minutes	Normal	Weight of fish in grams	Survival time of fish in minutes	Remarks
0.66	2.0	78	5.7×10^{-3}	3.2	62*	
"	2.7	85	"	3.2	137	
0.58	2.6	83	4.5×10^{-3}	2.5	58	
"	2.7	84	"	2.6	53	
0.43	3.0	85	2.6×10^{-3}	3.5	117	
"	3.1	85	"	5.0	128*	
0.33	2.0	45*	2.8×10^{-3}	2.8	59	
"	2.2	39	"	2.8	69	
0.25	2.2	38	2.3×10^{-3}	2.8	83	
"	3.0	30	"	3.3	80	
0.19	1.8	44*	1.8×10^{-3}	3.3	117	
"	1.95	49*	"	3.5	100	
0.15	2.8	92	1.2×10^{-3}	3.2	90	
"	3.2	52*	"	4.3	97	
0.11	2.7	96	9.1×10^{-4}	3.2	100	*Fish was alive when
"	3.0	70	"	3.5	140	taken out of solution.
0.068	1.9	85	4.5×10^{-4}	2.9	120*	
"	1.9	87	"	2.9	136	
0.034	1.7	133	2.2×10^{-4}	3.8	112	
"	1.9	118	"	4.1	116	
0.023	3.5	44*	1.1×10^{-4}	3.7	158*	
"	4.0	56*	"	3.8	112	
0.017	2.1	60*	0.56×10^{-4}	4.1	125	
"	2.3	66	"	4.2	260	
"	2.5	80	0.19×10^{-4}	3.0	214	
"	3.8	63	"	3.3	±300	
0.011	2.8	52*	0.13×10^{-4}	3.5	±315	
"	3.2	51*	"	3.9	367	
9.1×10^{-3}	2.5	146	0.34×10^{-5}	3.9	117*	
"	2.5	164	"	3.9	208	
7.9×10^{-3}	2.9	115*	0.11×10^{-5}	2.8	±300	
"	3.2	59*	"	3.9	403	
5.7×10^{-3}	3.4	70	0.28×10^{-6}	3.1	216	
"	3.5	70	"	4.4	430	

TABLE XXVI

CADMIUM CHLORIDE. TEMPERATURE 21.5°C.

Normal	Weight of fish in grams	Survival time of fish in minutes	Normal	Weight of fish in grams	Survival time of fish in minutes	Remarks
0.157	1.95	68	0.92×10^{-3}	3.2	167	
"	2.0	70	"	4.5	177	
0.1191	1.6	59*	0.42×10^{-3}	3.0	169	
"	2.0	61	"	4.3	204	
0.1036	1.7	61	0.24×10^{-3}	3.8	272	
"	2.3	62	"	4.0	208	
0.0903	1.65	59	0.12×10^{-3}	3.0	163	
"	1.75	39	"	4.0	165	
0.078	1.9	43	6.6×10^{-5}	2.8	148	
"	2.0	42	"	2.9	189	
0.065	1.9	54	3.7×10^{-5}	2.7	215	
"	2.0	57	"	4.1	292*	
0.057	1.9	59	1.8×10^{-5}	3.0	325	
"	1.9	60	"	4.1	126	
0.048	1.7	75	1.1×10^{-5}	4.4	349	
"	2.1	77	"	4.5	400	
0.043	1.7	73	0.74×10^{-5}	3.0	248	
"	1.9	67	"	3.0	335	*Fish was not dead when taken out of solution.
0.037	1.5	41	0.37×10^{-5}	3.9	360	
"	1.9	82	"	4.0	349	
0.032	1.65	78	"	3.6	199	
"	1.7	81	"	3.6	224	
0.024	1.8	120	0.18×10^{-5}	4.0	311	
"	2.0	121	"	4.7	261	
0.021	1.6	93	"	2.9	237	
"	1.75	100	"	3.8	349	
0.018	1.9	102	9.2×10^{-7}	3.8	335	
"	2.7	118	"	4.3	373	
0.015	1.6	164	5.2×10^{-7}	4.1	286	
"	2.15	136	"	4.6	316	
6.6×10^{-3}	2.0	132	2.6×10^{-7}	3.6	445	
"	2.9	130	"	4.6	353	
"	3.7	206	1.3×10^{-7}	3.4	635	
"	3.7	216	"	3.7	635	
3.7×10^{-3}	1.9	115	0.74×10^{-7}	4.7	861	
"	2.0	135*	"	5.5	±960	
"	3.4	233	0.37×10^{-7}	3.7	442	
"	3.6	295	"	3.8	479	
1.8×10^{-3}	3.4	193*	0.18×10^{-7}	3.9	±1080	
"	3.7	206	"	4.3	523	

trations (0.66 to 0.25 N. See Table XXV) increased with decrease in concentration. The shortest survival time of any goldfish was 30 minutes. From this point (0.25 N.) the toxicity of the $CuCl_2$ decreased with decrease in concentration but the decrease was very slight as compared to the dilution until the maximum survival time of the goldfish was 430 minutes. With the $CdCl_2$ there was also an increase in toxicity with a decrease in concentration with the highest concentrations tested (0.157 to 0.078 N. See Table XXVI). The two goldfish died in 42 and 43 minutes in 0.078 N. $CdCl_2$. From this point

TABLE XXVII
FERRIC CHLORIDE. TEMPERATURE 21.5° C.

Normal	Weight of fish in grams	Survival time of fish in minutes	Normal	Weight of fish in grams	Survival time of fish in minutes	Remarks
0.284	2.1	28*	8.32×10^{-3}	1.8	89	
"	2.3	29	"	1.9	109	
0.213	1.5	26*	"	3.3	247	
"	1.7	28	"	3.6	115	
0.159	1.7	26*	3.88×10^{-3}	2.8	101	
"	2.2	31	"	3.2	127	
0.119	1.5	38*	"	2.1	121	
"	1.8	32	"	2.1	129	*Fish was not dead when taken out of solution.
0.0693	1.7	33*	1.94×10^{-3}	3.0	131	
"	3.0	43*	"	3.4	113	
0.0554	1.9	46*	1.1×10^{-3}	3.4	164	
"	2.1	38	"	3.6	180	
0.0332	1.8	56	5.5×10^{-4}	3.3	450	
"	2.2	59	"	3.9	723	
0.0166	1.7	84	2.8×10^{-4}	2.7	790	
"	2.1	74	"	3.4	±1080	
"	3.3	89	1.66×10^{-4}	3.0	±1200	
"	3.7	83	"	3.2	±1200	

the toxicity decreased very slowly in proportion to the dilution of the solution until the maximum survival time of the goldfish was 1080 minutes in 0.18×10^{-7} N. The toxicity of the $FeCl_3$, unlike $CuCl_2$ and $CdCl_2$, decreased progressively with the dilution of the solution from the highest concentration (0.284 N. See Table XXVII) to the lowest concentration (0.166×10^{-3} N.) tested when the survival time of the goldfish reached a maximum of 1200 minutes.

The variations of the toxicities of these three salts from that of other substances tested can possibly be explained by the fact that they form colloidal

solutions and that colloids are very toxic and that the amount of colloid in the solution is not in proportion to the concentration of the salt in solution. Miyake (1916) found 1/75000 N. $AlCl_3$ was toxic to the growth of rice seedlings which he attributed to colloidal $AlCl_3$. Robin (1914) showed that the toxic activity of colloidal sulphur was much more intense than that of other forms of sulphur. The maximum survival time of the goldfish in ordinary distilled water was about the same as that in the most dilute $CuCl_2$ tested. Mengarini and Scala have shown that numerous metals, like copper and aluminum, form colloidal solutions in distilled water at room temperature. The toxicity of the distilled water, since it was distilled in copper stills with block-tin leads, was due possibly to the colloidal $CuO \times H_2O$ and $SnO_2 \times H_2O$. Ringer (1883) found that goldfish would live from 46 to 54 hours in distilled water. Bullot (1904) found that the survival time of Gammarus was shorter in water

TABLE XXVIII
WATER DISTILLED IN A COPPER STILL WITH BLOCK-TIN LEADS TEMPERATURE 21.5° C.

Weight of fish in grams	Survival time of fish in minutes
3.4	352
3.8	512
3.9	597
4.3	367

TABLE XXIX
WATER DISTILLED IN GLASS

Weight of fish in grams	Survival time in days
2.7	41
?	51
?	30
3.2	37

TABLE XXX
COLLOIDAL COPPER TEMPERATURE 21.5° C.

Exp.	Weight of fish in grams	Survival time of fish in minutes
1	4.3	900
1	4.6	900
2	4.0	2880
2	4.9	2820

distilled in copper than in ordinary glass, Jena glass, quartz glass, and platinum. The latter were all toxic to about the same extent.

Three sets of experiments were run to test the supposition that a colloidal solution was responsible for the short survival time of the goldfish in ordinary distilled water. 1. The goldfish lived 36 days in distilled water after an electrolyte (0.025 N. NaCl) had been added to precipitate the colloid. 2. The goldfish lived 30 to 52 days in water distilled in ordinary glass. 3. A colloidal solution of copper was prepared in water distilled in ordinary glass by arcing copper wires under the surface of the water. To one quantity of water a smaller amount of colloidal copper was added and the goldfish lived about 2820 minutes. To another a larger amount of colloidal copper was added and the goldfish lived only about 900 minutes. Thus the greater toxic

activity of water distilled in copper stills with block-tin leads and possibly also the $CuCl_2$, $CdCl_2$, and $FeCl_3$ solutions is probably due to the presence of a colloid. This is in keeping with Locke's (1895) results in which he showed that distilled water may lose its toxic activity by long boiling, and especially when brought in contact with sulphur, carbon, manganic oxide, cotton, wool, silk, and other substances, and those of Wells (1915) who found distilled water no more toxic than tap-water so long as the distilled water was slightly acid.

THE EFFICIENCY OF THE GOLDFISH AS A TEST ANIMAL

In all substances tested the goldfish died fairly uniformly in any given concentration where the survival time did not exceed five hours. See Tables I to XXIV for data of experiments in which two goldfish were killed in each solution tested. The variation of the survival time is better shown by data of experiments given in Tables XXXI and XXXII in which a number of fish were killed in each solution. The broken line in Figure 21 is a graphic representation of the survival times of the 8 goldfish killed in 0.272 N. LiCl solu-

TABLE XXXI

THE VARIATION IN THE SURVIVAL TIME OF THE GOLDFISH. TEMPERATURE 20° TO 21° C.

0.272 N. Lithium Chloride		0.229 N. Ammonium Chloride		0.222 N. Ammonium Chloride		0 231 N. Potassium Chloride	
Weight of fish in grams	Survival time of fish in minutes	Weight of fish in grams	Survival time of fish in minutes	Weight of fish in grams	Survival time of fish in minutes	Weight of fish in grams	Survival time of fish in minutes
1.9	79	2.3	49.5	2.5	51	1.5	17
2.0	78	2.4	49.5	2.6	62	2.3	51
2.2	88	2.6	52	2.65	71	2.5	49
2.2	89*	2.6	74	2.7	51	2.5	43
2.25	87	2.8	53	2.9	78	2.55	69
2.3	81	2.9	54	2.9	85	2.6	69
2.4	70	2.0	88	2.9	126	2.8	47*
2.4	86	3.0	69	3.0	69	2.8	48
		3.1	104				

*Fish was not dead when taken out of solution

tion, Table XXXI. One block of abscissa represents an individual goldfish and one block ordinate represents 100 minutes survival time of the goldfish in the 0.272 N. LiCl. The goldfish with the shortest survival time is represented first and the second next and so on to the goldfish with the longest survival time. Thus the deviation of the line from the horizontal represents the variation of the survival time of the goldfish in the given solution. Each of the other lines of the graphs in Figures 21 and 22 represents the survival times of individual goldfish in a definite concentration of a particular substance tested. In all graphs one block ordinate represents 100 minutes survival time and one block abscissa represents an individual goldfish. In these

graphs the weight of the goldfish is not taken into consideration. The goldfish with the shortest survival time is always considered first, the second next, and so on. Small variations in the weight of the goldfish had very little effect on their survival time, though in general the smaller died first. Of all goldfish killed the smaller died first in the ratio of 2.1 to 1. Where there was a greater variation in size the smaller died first in a much greater proportion. For variations of the survival time of the goldfish as compared to their relative weights see Tables I to XXXVI. In all the tables the smallest goldfish is placed first, the next smallest second, and so on.

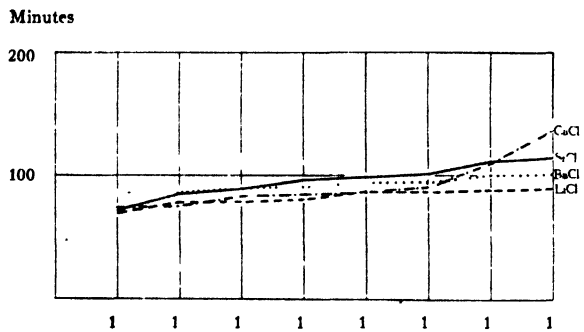


Figure 21. Graph showing the efficiency of the goldfish as a test animal. Ordinate represents the survival time in minutes and abscissa represents individual fish

Dot and dash line = 0.284 N. $CaCl_2$
Solid line = 0.274 N. $SrCl_2$
Dotted line = 0.214 $BaCl_2$
Broken line = 0.272 N. LiCl

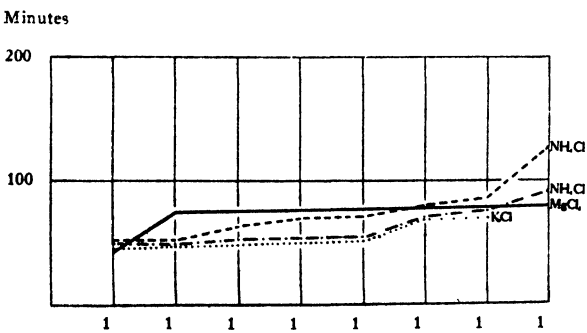


Figure 22. Graph showing the efficiency of the goldfish as a test animal

Broken line = 0.222 N. NH_4Cl
Dot and dash line = 0.229 N. NH_4Cl
Solid line = 0.318 N. $MgCl_2$
Dotted line = 0.231 N. KCl

THE EFFECT OF TEMPERATURE UPON THE RESISTANCE OF GOLDFISH

A few experiments were run to determine the effect of temperature on the toxic activity of a substance on the goldfish. It is shown by Tables XXXIII, XXXIV, and XXXV that the survival time of the goldfish in a constant concentration of a substance is lowered by a rise in temperature. This agrees with other workers on toxicity. See bibliography for citations. No attempt was made to find the relation between temperature and the toxic activity of a substance. See discussion of Warren's (1900) temperature toxicity curve, page 52.

TOXICITY AND THE EXPRESSION OF RELATIVE TOXICITY

The relative toxicity of the respective elements has long interested the chemist. The views of workers on the toxic activity of the elements have varied from time to time to fit any newly discovered physico-chemical conception of the properties of the elements. James Blake (1883, 1887) associated the physiological action of the elements of the isomorphous groups with their atomic weights. Botkin (1885) suggested a relation between the toxic activity of the elements and their position in the periodic system. Pauli (1903), Kahlenberg and True (1896), Kahlenberg and Austin (1900), Loeb (1902), and Mathews (1903, 1907) held that the toxic activity of a substance is dependent either upon the free electrical charge or the atom itself while in the atomic state. Richet (1881) and Rabuteau have suggested that toxicity is a function of the solubility of the substance. Mathews (1904) has related toxicity to the solution tension of the ion. While, finally, Bert (1871), Garrey (1905), Křiženecký (1916) and others claim that the toxic effect of at least certain elements to fresh water animals is due primarily to osmotic pressure. After all these and other suggestions such as coagulation of the protoplasm, ionic combination, either physical or chemical, with the protein of the protoplasm, and the change of permeability of the cell membrane, the cause of toxicity is still an open question. Aside from the divergence of opinions as to the cause of the active properties of the elements there has been no absolute agreement on relative toxicity itself. In this work some attempt has been made to determine the relative toxic values of certain of the alkali and alkaline earth metals when in combination with Cl and NO_3. First it is obvious that it is necessary to have some standard of measure of the elements themselves. The elements will be arranged differently from the same data when considered by actual weight of the element, actual weight of the salt, molecular concentration, and normality. This of itself explains certain of the disagreements among workers, though after all the elements are reduced to a common standard of measure there is still a wide divergence in relative toxicity as reported by different workers. Osterhout (1915) has pointed out that "the relative toxicity of two substances may depend very largely on the stage of the reaction at which the measurement is made"; i.e., the criterion employed. Osterhout objects

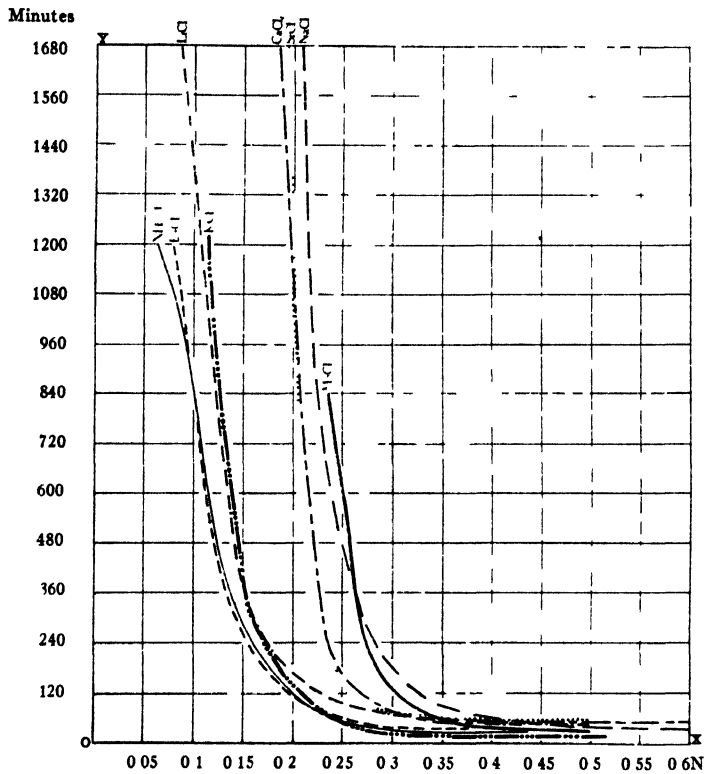


Figure 23 Superimposition of survival time curves of the alkali and alkaline earth metals as chlorides showing crossing over of curves, thus showing varying relative toxicities of the group when different definite survival periods are taken as a criterion.

to the utilization of the death point as a criterion and points out the fact that "it is impossible to determine the precise moment of death." He has shown that the death curve "approaches the axis asymptotically." He suggests that it may be assumed that as the reaction proceeds certain phenomena appear at definite points on the curve. He took as his criterion a point on the curve at which he said that the organism was "half dead." The writer has found the same objections pointed out by Osterhout but has come to the conclusion that the death point with certain precautions is a more exact criterion for an end point in the case of the goldfish than the loss of equilibrium or irritability. Aside from the objections raised by Osterhout there is a still more serious objection to any attempt to determine relative toxicities by comparing the concentrations of the solutions or the amount of the substance necessary to produce death or the appearance of any physiological phenomenon in any arbitrary fixed time or the concentration necessary to just cause

death. The relative toxic activities of the substances will vary according to the criterion used. Only a glance at figure 23 is required to convince one that there will be a marked rearrangement in the relative toxic values of the elements when different survival times are used as criteria. For example, if a 120 minute survival time is chosen as a criterion the relative toxicities of the elements as chlorides with normality as the standard of measure will be arranged from the most toxic to the least toxic in the following order:—Ba, K, Li, Sr, Ca, Mg, and Na, and with a 60 minute survival time they will be arranged as follows:—K, Ba, Ca, Li, Sr, Mg, and Na. Thus there is a marked rearrangement of the relative positions of the elements with a change from a 120 minute survival time as a criterion to that of a 60 minute survival time. It is the opinion of the writer that it is the employment of different criteria that is responsible more than any other one thing for the differences of opinions of workers on the toxic values of the elements. The fact is not denied that the elements may have different relative activities toward different organs of the same animal as well as toward different animals (Kahlenberg and Mehl 1901). By a study of the survival time curves shown in Figure 23 it is seen that the activity of each element is a law unto itself, and thus there is no one expression that will include all specificities of the salts or toxic substances. But a standard criterion may be derived. From a study of the velocity of fatality curves it is seen that there are two variables and that these vary independently of each other. 1. The concentration necessary to just kill the goldfish varies with the element. 2. The acceleration of the change of direction of the survival time curve, i.e., the increase in the velocity of fatality is different in each of the salts and does not necessarily have any relation to the amount of the salt necessary to just kill the goldfish. The value of the first factor is shown by the position of the point C and the second by the slant of the velocity of fatality curve. But since the slant of the velocity of fatality curve is not uniform for all concentrations of a substance the theoretical velocity of fatality curve will be considered. This curve bears the same relation to the physiological activity of the substance as the true velocity of fatality curve. Thus the relative toxicities of substances due to the first factor can be measured by the reciprocal of a, the distance P from the origin O. That due to the second can be measured by the tangent of the angle XPB, θ. (See Figure 1.) Both these factors must be taken into consideration in a criterion or an expression representing the relative toxicity of a substance. The tangent θ increases as the toxicity increases with respect to the slope of the theoretical velocity of fatality curve, i.e., the rapidity with which the activity of the substance increases with increase in concentration and the distance of the point P from the origin O or a decreases as the toxicity increases with respect to the theoretical threshold of toxicity concentration, i.e., as the theoretical threshold of toxicity concentration decreases. Thus it is seen that these two factors are the reciprocal of each other. This relation can be expressed mathematically by the equation,

T (toxicity) $= \sqrt{\frac{\text{tan. } \theta}{a}}$ This equation cannot represent the absolute or the exact relative toxic value of a substance since it is based only on a portion of the velocity of fatality curve, the portion A to B, Figure 1, and the assumption that this portion and the two extremes, i.e., the two extremes C to A and B to G, follow the reciprocal of an equilateral hyperbola which is not in keeping with experimental data or a curve drawn from the hypothetical equation representing the true velocity of fatality curve. See pages 48, 52 for a discussion of this hypothetical equation. However this expression has been chosen to represent the relative toxic value of a substance rather than the curve itself as suggested by Osterhout (1915), as the latter leaves the formation of a criterion to the reader. It has the advantage in that the relative toxicity can be given a numerical value and is a natural criterion and not an arbitrary one. This equation, as has already been pointed out, does not express the specificity of the toxic activity of the salt, which can be shown only by the curve itself, as Osterhout has suggested, or by taking into consideration the factors which go to make up an equation which represents the curve itself (See hypothetical equation page 49). Taking the above equation as representing the relative toxicities of the alkali and alkaline earth metals, as chlorides and nitrates, the toxic values are found as given in Table XXXVI. These values are comparable in general, not so much in comparative numerical values but in position, to values obtained by other workers after the measurements of the elements are reduced to a common standard. See bibliography for citations. However, among all workers there is more or less difference of opinion.

TABLE XXXVI

RELATIVE TOXICITIES OF THE ALKALI AND ALKALINE EARTH METALS WHEN IN COMBINATION WITH Cl AND NO_3

Substance	Relative toxicity
NaCl	1.24
LiCl	1.53
KCl	2.3
NH_4Cl	2.87
$CaCl_2$	1.56
$SrCl_2$	1.57
$MgCl_2$	1.87
$BaCl_2$	1.94
$NaNO_3$	1.00
NH_4NO_3	1.95
$Mg(NO_3)_2$	1.75
$Ca(NO_3)_2$	1.92
$Sr(NO_3)_2$	2.58

IS THE TOXICITY OF A SUBSTANCE DUE TO OSMOTIC PRESSURE?

A series of experiments was run with d-glucose (Table XXXVII) to determine the effect of osmotic pressure on the goldfish. When the molecular concentration of the glucose is divided by two to make its osmotic pressure comparable to that of a normal salt solution, it is seen that the toxicity of the glucose is still below that of the particular salt to which it is compared. This difference is even more striking when the fact that the salts are not completely ionized is taken into consideration and that this is more than sufficient to allow for complete ionization of salts of bi and tri valent acids and bases. The improbability that the toxicity of a substance is due to osmotic pressure is further emphasized by the fact that the toxic activities of substances like potassium cyanide, hydrochloric acid, the alcohols, caffeine, phenol, and pyridine are not in proportion to their molecular concentrations.

TABLE XXXVII
D-GLUCOSE. TEMPERATURE 21.5°C.

Mole	Weight of fish in grams	Survival time of fish in minutes	Mole	Weight of fish in grams	Survival time of fish in minutes
1.	2.3	158	0.15	2.4	5700
"	2.7	77	"	2.3	7140
0.6	2.5	311	0.075	3.0	5640
"	3.8	356	"	3.3	7860
0.4	2.7	±1200	0.05	2.8	2880
"	3.2	±2640	"	4.7	4560
0.2	2.2	±8400	0.025	2.8	2880
"	2.9	±8400			

THEORY OF THE POISONING EFFECT ON TOXIC SUBSTANCES

Osterhout (1915) has shown in a very interesting paper that death in the Laminaria, when placed in NaCl solution of the same conductivity as that of sea-water, as measured by the fall of electrical resistance, does not follow a straight line when electrical resistance is plotted as ordinate and time as abscissa, but follows a curve which, he points out, "follows the course of a monomolecular reaction."

The effect of poison on protoplasm might be compared to a system of chemical reactions which finally result in the death of the organism. It has been shown outside the living organism that KCN retards oxidation. Kastle

and Loevenhart (1901) pointed out the fact that the activity of oxidase of the potato was retarded by KCN. Shafer (1915) found that hydrocyanic acid affects catalases, reductases, and oxidases in insect tissues. Mathews and Walker (1909) showed that very small amounts of KCN is sufficient to check or prevent the spontaneous oxidation of cysteine to cystin both in neutral and alkaline solutions. Loevenhart and Kastle (1903) have shown that hydrocyanic acid inhibits the catalytic activity of solutions of metallic colloids. Claud Bernard (1857) noted that venous blood of an animal poisoned with hydrocyanic acid takes on an arterial hue. Geppert (1889) showed venous blood to have a higher oxygen content than normal in mammals poisoned with hydrocyanic acid. Richards and Wallace (1908) found that protein metabolism is increased in a dog by poisoning with KCN due in part to the retarding effect on oxidation by the KCN. Loeb and others have shown that oxygen requirement is decreased and that this decrease is greater the greater amount of KCN used. All have shown that KCN in very small amounts acts as a stimulus to oxidation both in and out of the animal organism. Moore and Moore (1917) have shown that the maturity of fruit was two weeks earlier and that the total yield of fruit was larger on tomato plants fumigated with HCN than normal plants. Woodworth (1915) showed that scale insects eggs when fumigated with hydrocyanic acid in amounts not sufficient to kill them hatched earlier than the normal eggs. Townsend (1901) has found that there is an increase in germination in seed fumigated with hydrocyanic acid. And Zieger (1915) in turn has shown that the activity of the catalase is in proportion to the general metabolic activities in animals. While Child (1915, p. 66 and citations) and others have shown that very small amounts of KCN increase the rate of metabolism while larger amounts decrease metabolic processes, Mathews (1916, p. 813) suggests that since cysteine oxidizes itself and has many points in its oxidation which resemble respiration there is more than a superficial connection between the oxidation of cysteine and the respiration of the cell. The most favorable hydrogen ion concentration for oxidation is the same as that of protoplasm and both cysteine and protoplasm are poisoned by many of the same substances, as nitriles, the cyanides, acids, and heavy metals. Their oxidations are catalyzed or hastened in the same manner by iron, arsenic, and certain other agents. Burge and Burge (1914, 1915) have shown that digestion of a dead round worm in activated pancreatic juice does not take place so long as its body wall is constantly permeated with nascent oxygen. They conclude that the oxidative processes of living parasites enable them to withstand the enzymes by oxidizing the enzymes in contact with them. Lillie (1902) advances the theory that the tissues are protected from autolysis by oxidizing the enzymes in contact with them. Hofmeister (Mathews 1916, p. 83), Verworn (1909, p. 53), Hopkins (1914), and others have held that there is no vital matter in the cell and that the chemical transformations do not involve any large biogene molecule but only relatively simple compounds in solution. But Pflüger, Du Bois-Reymond (Mathews,

1916, pp. 842-844), Driesch (1909), and Sir Oliver Lodge (1913) suggest that there is an organized force, entelechy, or vital force and that so long as the cell is alive this force regulates the metabolism but as soon as this force is destroyed or inhibited the metabolic processes cease, i.e , the machinery no longer works and the cell dies. Robertson (1908) suggests that the normal rate of growth is an autocatalytic process. And finally Troland (1917) defends the thesis that all biological enigmas as he calls them are explainable on the basis of enzymes either autocatalytic or heterocatalytic. Thus it appears from either the mechanistic or the vitalistic view and experimental data that metabolism can be conceived of as a self-perpetuating mechanism and that when metabolism is interfered with beyond a certain limit, this mechanism or metabolism is progressively depressed or inhibited. That is, metabolism continues within a certain limit at a normal rate; enzymes, excitors, or antibodies inhibiting autolysis are liberated or generated which stimulate metabolism or allow metabolic activities to continue at a normal rate. But as rapidly as the rate of metabolism is reduced below this normal rate, beyond a certain limit, the rate of liberating or generating enzymes or antibodies is reduced in proportion to the reduction of the rate of liberation or generation of the cell enzymes or antibodies. In other words, we are dealing here with the rate of inhibition of a process, metabolism, the rate of which is uniform under any fixed set of normal conditions. One of the factors of a normal condition is a normal rate of metabolism. Thus when the rate of metabolism is reduced below the normal the conditions become abnormal. This in turn becomes an inhibiting factor which increases progressively with the decrease in the rate of metabolism, i.e., it becomes self-inhibiting. This portion of the effect on the speed of inhibition of metabolism is thus proportional to the product of the amount of reduction in the rate of metabolism at any time t, and the reduced rate of metabolism at that time. This can be compared in the speed of the reduction of the rate of metabolism to the velocity of an autocatalytic reaction and can thus be expressed mathematically $\frac{dz}{dt} = K_2 z(M-z)$. That is, at any given time, t, the speed of inhibition of metabolism is in proportion to the product of the reduced rate of metabolism and the rate of metabolism at the given time. M = normal rate of metabolism under any fixed set of conditions, z = amount of reduction of rate of metabolism at any given time, K_2 = a constant representing the efficiency of the reduced rate of metabolism in inhibiting metabolic processes, i.e., in inhibiting the activation or action of the metabolic enzymes or antibodies or representing the liberation of autolytic enzymes, and t = time. The amount of reduction z in the rate of metabolism after any time t is due not only to the autoinhibitory process but also to the continuous action of the protoplasmic poison introduced. But the equation above takes into consideration only the reduction due to the autoinhibitory process, and does not take into

consideration the continuous action of the poison on the rate of reduction of metabolism. But at any given time the speed of reduction of the rate of metabolism due to the continuous action of the protoplasmic poison is in proportion to the amount of poison acting at the given time and the actual rate of metabolism, i.e., (M-z). Thus the speed of the inhibition of the rate of metabolism by the continuous action of the protoplasmic poison can be compared to the velocity of a simple mass action. And since the fish is in a solution the volume of which is large as compared to the volume of the fish and since the poison is continuously diffusing into the protoplasm to the point of equilibrium, the amount of protoplasmic poison can be considered as constant throughout the entire process. The equation representing the speed of reduction of rate of metabolism by the continuous action of the protoplasmic poison then becomes $\frac{dz}{dt} = K_1X(M\text{-}z)$. K_1 = the efficiency of the protoplasmic poison in reducing the rate of metabolism and X = the amount of poison employed and is a constant for any definite amount of poison employed and appears in the equation only for the sake of comparing the action of different amounts of protoplasmic poison employed in any two experiments.

Since both of the processes indicated by the above equations are acting simultaneously to reduce the rate of metabolism, the actual rate of reduction is the sum of the two left members. If we now denote this actual rate of reduction by $-\frac{dz}{dt}$, then $\frac{dz}{dt} = K_1X(M\text{-}z)+K_2z(M\text{-}z)$.

Integrating we have t+C (constant of integration) = $\frac{1}{MK_2+K_1X}\log_e \frac{K_1X+K_2z}{K_2(M\text{-}z)}$

But when t=0, z=0. Then $C = \frac{1}{MK_2+K_1X}\log_e \frac{K_1X}{K_2M}$.

By substituting the value of C and transforming we have:

$$t = \frac{1}{MK_2+K_1X}\log_e \frac{K_1X+K_2z}{K_2(M\text{-}z)} - \frac{1}{MK_2+K_1X}\log_e \frac{K_1X}{K_2M} =$$

$$\frac{1}{MK_2+K_1X}\log_e\left(\frac{M}{M\text{-}z}+\frac{K_2Mz}{K_1(M\text{-}z)}\cdot\frac{1}{X}\right).$$

$$\text{Or } \frac{1}{t} = Y = \frac{MK_2+K_1X}{\log_e\left(\frac{M}{M\text{-}z}+\frac{K_2Mz}{K_1(M\text{-}z)}\cdot\frac{1}{X}\right)}$$

The reciprocal of the survival time of the goldfish $\frac{1}{t}$ is represented as ordinate in the graphs of the velocity of fatality curves, thus $\frac{1}{t} = Y$

Any mathematical expression of the velocity of fatality curve must comply both with actual experimental data and with theoretical demands. 1. The mathematical expression should show that the velocity of fatality increases very slowly with increase in concentration when very low concentrations of the poison are used. 2. It should show that the velocity of fatality increases very rapidly with an increase in concentration when higher concentrations of poison are used. 3. Finally with still higher concentrations of the poison it should show a less rapid increase in velocity of fatality with increase in concentration. 4. At very high concentrations of poison it should show that the velocity of fatality curve approaches a straight line. See discussion page 43.

When X varies in the equation $Y = \frac{1}{t} = \frac{K_2M+K_1X}{\log_e (\frac{M}{M-z} + \frac{K_2Mz}{K_1(M-z)} \cdot \frac{1}{X})}$ and all other factors on the right hand side of the equation remain constant, it is found that when X is very small so that K_1X is very small as compared to K_2M the numerator (K_2M+K_1X) approaches a constant. Thus the value of $\frac{1}{t}$ or Y is controlled by the reciprocal of the logarithm of a number which is controlled by the reciprocal of X, i.e., $\log_e (\frac{M}{M-z} + \frac{K_2Mz}{K_1(M-z)} \cdot \frac{1}{X})$. When X is neither very large nor very small as compared to the other factors neither the numerator nor the denominator approaches a constant and Y is controlled by the increase of X in the numerator and the reciprocal of the logarithm of a number which is increased by the reciprocal of X. Finally, when X is very large the denominator $\log_e (\frac{M}{M-z} + \frac{K_2Mz}{K_1(M-z)} \cdot \frac{1}{X})$ approaches a constant, $\frac{M}{M-z}$ becomes very large as compared to $\frac{K_2Mz.}{K_1(M\ z)} \cdot \frac{1}{X}$. Thus Y is controlled by the increase of X in the numerator (K_2M+K_1X) since K_1X is large as compared to K_2M. From these three conditions it is seen that the value of Y at first increases very slowly, being controlled by the reciprocal of the logarithm of the reciprocal of a number. After this it increases more rapidly, being increased by the same factor as the first and in addition is increased by a multiple of the number itself, i.e., numerator (K_2M+K_1X). Finally, in the third case Y increases only by some multiple of the number since X is very large as compared to $\frac{K_2Mz}{K_1(M-z)}$ the expression $\frac{K_2Mz}{K_1(M-z)} \cdot \frac{1}{X}$ approaches zero. Thus it is seen when $\frac{1}{t}$ or Y is plotted as ordinate and X as abscissa a curve, the velocity of fatality curve, will be formed which at first has a very gradual rise followed by a rapid rise which again is followed by a less rapid rise depending on the value of K_1X which finally approaches a straight line at very high values of X. This curve

will approach a straight line where the direction of the curvature changes (See the portion A to B, curve CABG, Figure 1). The nearness with which this portion approaches a straight line depends on the values of M, K_1, and K_2 as compared to X. Thus the theoretical velocity of fatality curve complies with the actual experimental velocity of fatality curve.

The above equation though conforming in a general way to the experimental data, is doubtless incomplete. It is only an attempt at a mathematical expression which might be taken to represent the experimental data and should be corrected for other factors not taken into consideration here.

The validity of the equation is further emphasized by the work of Burge (1917) in which he shows that both ether and chloroform not only destroy the catalase of the blood of an anesthetised animal but also inhibit the production or the liberation of the catalase by the liver. In other words there are two factors. One is the effect of the poison in inhibiting the liberation or production of an enzyme and the other is the continuous action of the poison in destroying the enzyme which has already been formed or liberated. Both these factors are expressed in the theoretical equation.

A mathematical study of the equation shows that as X decreases in value, Y becomes zero. This value of X corresponds to the threshold of toxicity concentration. When X is decreased below this point, Y becomes imaginary. This is in keeping with experimental data, as very small amounts of certain active substances do not inhibit but stimulate metabolic processes.

COMPARISON OF CURVES OBTAINED BY OTHER WORKERS

Warren (1900) in his work on Daphnia was first to call attention to the fact that when aquatic animals are killed by placing them in solutions of a toxic substance if the survival time is plotted as ordinate and the concentration of the solution as abscissa, the points when joined will form a curve closely resembling an equilateral hyperbola. Warren considered all of his data as complying with this curve. Either he experimented with solutions which would fall within the concentrations where the velocity of fatality curve approaches a straight line or he disregarded data obtained outside this range of concentrations. Warren saw the similarity between his curves and the curves representing Boyle's law and explained his results by supposing that the toxicity of a substance above a definite amount (the writer's theoretical threshold of toxicity concentration) depended upon the number of molecules which beat on the body of the Daphnia per unit of time. Ostwald (1905, 1907) was next to call attention to a similar curve formulated from data obtained by killing Gammarus in different concentrations of sea-water or the constituents of sea-water. Ostwald, disregarding the extremes of his data, claimed that the curve was not an equilateral hyperbola and applied the modified absorption formula, $tC^n = K_1$ or $t(C\text{-}n)^m = K_1$ (Ostwald 1907) (see page 33). Křiženecký (1916) next noted the resemblance to that of an autocatalytic curve of a curve which he obtained by determining the time required for an annelid worm, *Enchytraeus humicultor*, to recover in ordinary tap water after having been in a solution of a toxic substance for one minute, when time was plotted as ordinate and concentration of the solution as abscissa. The curve obtained by Křiženecký resembles the writer's velocity of fatality curve. Křiženecký explained his results in terms of osmotic pressure. Clayberg (1917) called attention to such a curve and called it an hyperbola but made no attempt to show how nearly it approached an hyperbola or its variations. None of these workers have seen the significance of the entire curve nor did they construct what is designated by the writer as the velocity of fatality curve. Neither did they suggest the possibility of its utilization in physiological testing nor attempt to connect their entire data with life processes. Gregersen (1916) in his investigation on the antiseptic value of gastric juice found that the disinfecting value of gastric juice was in direct proportion to the free acidity and that the product of the survival time of the bacteria and the titration number was almost constant. This in fact represents an equilateral hyperbola but such a relation was evidently not noted by Gregersen. Warren also showed that when the survival time of Daphnia killed in a constant concentration of a toxic substance at different temperatures was plotted as ordinate and temperature as abscissa a similar curve was formed.

Krogh (1914, 1914a) and Sanderson and Peairs (1913) almost at the same time and independently of each other noted that a similar curve was formed when rate of development of eggs of frogs, insects and sea-urchins and also larvae and pupae of insects was plotted as ordinate and temperature as abscissa. Sanderson and Peairs determined the reciprocal curve which they designated as the rate of development and considered it a straight line crossing the X-axis at the actual zero of development. They disregarded the variations from a straight line at the extremes altogether and made all calculations on the assumption that the temperature above their theoretical zero times the time required for the organism to pass through certain stages of development is a constant. Krogh in his work called attention to the variations of the rate of development begun below the point at which the straight line cut the X-axis, i.e., the lowest temperature at which development will take place is below the theoretical temperature for the initiation of development. Reibisch (1902) called this the threshold of development.

Finally, Osterhout has shown that the dying curve of Laminaria when killed in an NaCl or a $CaCl_2$ solution of the same conductivity as that of sea-water as shown by the fall of electrical resistance after having passed the point of stimulation of the latter salt follows the course of the same general curve when resistance is plotted as ordinate and time as abscissa.

The close similarity of the curves found by different workers in entirely different fields suggests that the extremes of the reciprocal curves should be more thoroughly investigated. The possibility is that no portion of the curve is a straight line. This supposition is evidenced by the equation $1/t = (MK_2 + K_1X)/\log_e \left(\frac{M}{M-z} + \frac{MK_2z}{K_1(M-z)} \cdot \frac{1}{X}\right)$. This is further emphasized by the fact that Ostwald's data fits almost equally well the formulae $y(x-a) = k$, i.e., $1/t = (x-a)/K = K_1(x-a)$ and $t(C-n) = K_1$, i.e., $\log_e t + m\log_e (C-n) = \log_e K_1$. These two equations represent hyperbolae of entirely different orders and are never similar except when $m = 1$. Thus the evidence is that neither of the two equations fits exactly. But for all practical purposes in pharmaceutical work and in insect pest prediction (Shelford 1918) the equation $1/t = y = K_1(x-a)$ can be considered as holding in very narrow limits i.e., when the temperature to which the insect pest is subjected is never below the temperature at which the velocity of development curve ceases to approach a straight line; otherwise, some modification of the equation used by entomologists must be employed.

DISCUSSION OF DATA

All substances investigated show very striking similarities in their toxic activities on the goldfish. 1. All substances show a slow relative increase in rate of velocity of fatality with increase of substance used when time required for fatality is above 720 minutes. 2. The greatest rate of increase of velocity of fatality occurs when amounts of substances used will kill the goldfish in periods from about 45 minutes to about 210 minutes with only a few exceptions. (Table XXIV). 3. The rate of increase of velocity of fatality is less rapid with increase in concentration of the substance used when the time required to kill the goldfish is less than about 45 minutes. 4. When the velocity of fatality is plotted as ordinate and normality or the amount of substance used per liter as abscissa, the curve thus formed has a very striking resemblance to a monomolecular autocatalytic curve, i.e., it is a logarithmic curve. HCl and KCN show this character more strikingly than other substances tested as experiments were run over a large range of concentrations. (Figures 14 and 15.) 5. The velocity of fatality of the goldfish is more nearly constant for any given concentration when the concentration of toxic substances used is sufficient to kill the goldfish in a period of not less than 45 minutes nor more than 210 minutes, with very few exceptions. The range for KCN and HCl is from about 90 minutes to about 1800 minutes. This range must be determined independently for each substance. (Table XXIV.) 6. The velocity of fatality curve approaches a straight line for amounts of substances that will kill the goldfish in periods of time just mentioned. This range must be determined independently for each substance by the graphic method from experimental data. (Table XXIV and Figure 1 and explanatory notes.)

From these general results it is seen that when the toxic value or active principle of any substance is to be determined from a pharmacodynamic assay point of view; i.e., to determine the strength of an unknown, only such portions as will kill the goldfish within a range of a certain minimum and maximum time should be used. This range must have been previously determined for each substance to be tested. (See 5 and 6 above and Table XXIV.) An unknown can be determined by any one of five methods. 1. A definite survival time can be utilized, i.e., determine the concentration of the substance that will kill the goldfish in a selected period of time. The survival time of the goldfish for most exact determinations should be within the range of time where the velocity of fatality curve approaches a straight line. This range of time must have been previously determined for each substance to be tested. The portion A to B of the velocity of fatality curve, (Fig. 1 and Table XXIV.) This is a modification of the method proposed by Pittenger and Vanderkleed (1915). 2. A number of goldfish can be killed in the unknown and the average survival time taken and applied directly as ordinate to a survival time curve of the same

substance as that tested which has previously been very carefully prepared by killing a number of goldfish and placed in the hands of workers as a standard curve. For example, if the average survival time of a number of goldfish killed in an unknown LiCl solution was 150 minutes it is seen that the ordinate representing 150 minutes survival time will cut the LiCl survival time curve, LIJM (Fig. 1) at the point R and the normality (0.207 N.) of the LiCl solution. can be read directly from the abscissa. For this method to be most exact the point R must fall within the portion I to J of the survival time curve, i.e., the survival time of the goldfish must be within the portion of the curve where it corresponds to the portion of the velocity of fatality curve that approaches a straight line. 3. A number of goldfish can be killed in an unknown and the average of the survival time determined and data applied to the equation of an equilateral hyperbola, $y(x\text{-}a)=k$, where y=survival time of the goldfish, x= amount of substance used per liter, a=theoretical threshold of toxicity concentration, and k=a constant. For example the average survival time of a number of goldfish killed in an unknown LiCl solution is 150 minutes. By substituting in the equation the value of the constants (a=0.125 N. and k= 12.37 for LiCl) we have $150(x\text{-}0.125)=12.37$. Solving x=0.207 N. which is the strength of the unknown. k approaches a constant only when the velocity of fatality curve approaches a straight line. See Figure 1. The deviation of the velocity of fatality curve from a straight line increases progressively as the distance preceeding and following the portion A to B increases, and at the same time the survival time curve deviates from that of an equilateral hyperbola. Curve CABG, Fig. 25, is a graphic representation of this fact [See Shelford (1918) for detail of this curve]. Ordinate of curve represents k [$k=y(x\text{-}a)$]. If the survival time required to kill the goldfish is less than 45 minutes k is greater than 12.37 and if it requires longer than 210 minutes k is less than 12.37. Thus to apply this equation to LiCl the survival time of the goldfish must not be less than 45 minutes nor longer than 210 minutes. This range of survival time must have been previously determined for each substance to be tested. 4. Curve CABG, Fig. 25, when time is interpolated on abscissa (see abscissa at top of graph), can be utilized directly to determine the strength of the unknown, both where k approaches a constant and where k is a variable. Thus to determine the strength of an unknown apply the average survival time of a number of goldfish which have been killed in the unknown to the curve CABG, Fig 25, and read the normality of the unknown directly from the abscissa. For example, if the average survival time of the goldfish killed in an unknown LiCl solution is 150 minutes it will be found that this corresponds to the point R of the curve CABG. Then read directly from the abscissa 0.207 N. which is the strength of the unknown LiCl solution. Again for most exact determinations, concentrations represented from A to B must be used. This curve is of special interest and value in that it emphasizes the variability of k. 5. A few experiments can be run with different concentrations of the substance to be tested and the survival time of the goldfish in each experiment

determined. All concentrations used must fall within the range of concentrations where the velocity of fatality curve approaches a straight line. (Concentrations represented from A to B, curve CABG, Fig. 1). A graph should then be drawn with reciprocal of survival time as ordinate and the ratio of the substance used as abscissa (i.e., the theoretical velocity of fatality curve) on some standard scale. This curve which is practically a straight line and should be drawn as a straight line should then be compared to a standard curve which has been previously prepared from experimental data of the same substance at the same temperature or a curve drawn from data of experiments testing a known solution or standard of the same substance where a standard solution is available. The latter eliminates any error due to seasonal variation, variation in stock of goldfish, physiological state of the goldfish as well as variations in temperature at which the experiments can be run. Then the strengths of the known and the unknown solutions are inversely proportional to the distances from the origin O at which their theoretical velocity of fatality curves cut the X-axis. That is, the strength of the unknown solution is to the strength of the known solution as the distance from the origin O to the point where the theoretical velocity of fatality curve of the known solution cuts the X-axis is to the distance from the origin O to the point where the theoretical velocity of fatality curve of the unknown solution cuts the X-axis. For example, let e=strength of the known solution represented by the theoretical velocity of fatality curve SMP, Fig. 24, v=strength of an unknown solution No. 1, represented by the theoretical velocity of fatality curve SP′M′, and u=the strength of an unknown solution No. 2, represented by the theoretical velocity of fatality curve SP″M.″ Then $v{:}e{:}u = \frac{1}{OP'} : \frac{1}{OP} : \frac{1}{OP''} = \frac{1}{b} : \frac{1}{a} : \frac{1}{c}$ where a=distance

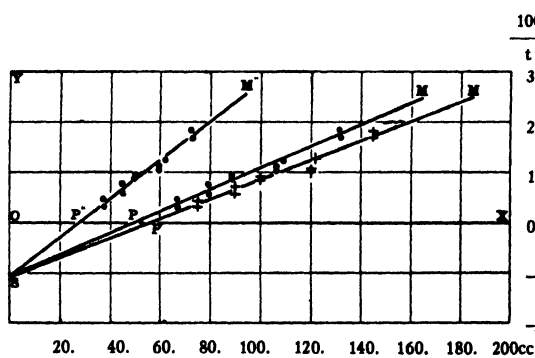


Figure 24. Lithium chloride. Graphs showing method of determining the normality of an unknown LiCl solution.

SPM = Theoretical velocity of fatality curve of a known solution of LiCl
SP′M′= " " " " " " an unknown " " No. 1
SP″M″= " " " " " " " " " " " 2

TABLE XXXVIII

LITHIUM CHLORIDE

cc. per liter	Survival time of fish in minutes	Reciprocal of survival time of fish 100/t	cc. per liter	Survival time of fish in minutes	Reciprocal of survival time of fish 100/t	cc. per liter	Survival time of fish in minutes	Reciprocal of survival time of fish 100/t
Known Sol.			Unknown Sol. No. 1	Calculated		Unknown Sol. No. 2	Calculated	
127.6	54	1.85	145	54	1.85	72.25	54	1.85
"	58	1.72	"	58	1.72	"	58	1.72
106.9	82*	1.27	121.5	82*	1.27	60.73	82*	1.27
105.6	92	1.08	120	92	1.08	60.0	92	1.08
"	96	1.04	"	96	1.04	"	96	1.04
88	116	.86	100	116	.86	50	116	.86
"	112	.89	"	112	.89	"	112	.89
79.2	141	.71	90	141	.71	45	141	.71
"	179	.56	"	179	.56	"	179	.56
66	234	.43	75	234	.43	37.25	234	.43
"	310	.32	"	310	.32	"	310	.32

*The average survival time of 8 goldfish

This table is based upon calculations from actual experimental data taken from tables I and XXXI

OP, b=OP', and c=OP''. The theoretical velocity of fatality curves can be better drawn and compared when it is remembered that all theoretical velocity of fatality curves of any one substance when drawn on a definite scale representing the reciprocal of the survival time of the goldfish and variable scales representing amounts of substance used per liter or normality of substance have a definite common point of intersection. That is, if the survival time of the goldfish be plotted as ordinate, and the number of cc. or g. per l. of known and unknown used be plotted as abscissa the curves thus formed would constitute a system of confocal conics of equilateral hyperbolae each being dragged out of position a distance OP, OP', and OP'' respectively. Therefore the reciprocal curves will all intersect on the Y-axis at the point S. (Fig. 24).

For example two hypothetical unknown LiCl solutions could be determined in the following manner. Make up six solutions from a known LiCl solution as given in the following table and determine the survival time and the reciprocal of the survival time of the goldfish in each solution as recorded. Test the unknown solutions No. 1 and No. 2 as shown in table XXXVIII. Plot a theoretical velocity of fatality curve for each set of data with reciprocal of survival time as ordinate and cc. of a solution used per l. as abscissa 1:100/t is used instead of 1/t to avoid the use of fractions. One block ordinate=1 velocity of fatality. One block abscissa=10 cc. of solution per l.

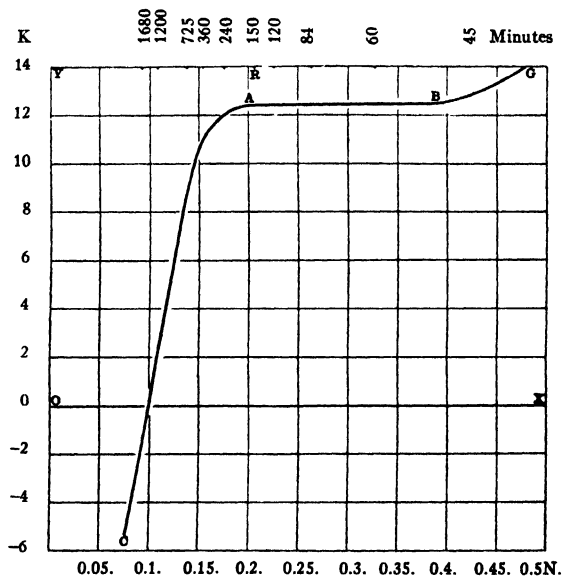


Figure 25. Lithium chloride. Graph showing curve when normality is plotted as abscissa and concentration minus the theoretical threshold of toxicity concentration, times survival time of the goldfish is plotted as ordinate, i.e., k of the equation $y(x-a)=k$. The graph shows the deviation of k from a true constant. The portion AB is equivalent in range to AB of the velocity of fatality curve Figure 1. y=survival time of goldfish in minutes. x= normality of the LiCl solution. a=theoretical threshold of toxicity concentration=0.125 N. and k=a constant=12.37 which holds only between the two points A and B.

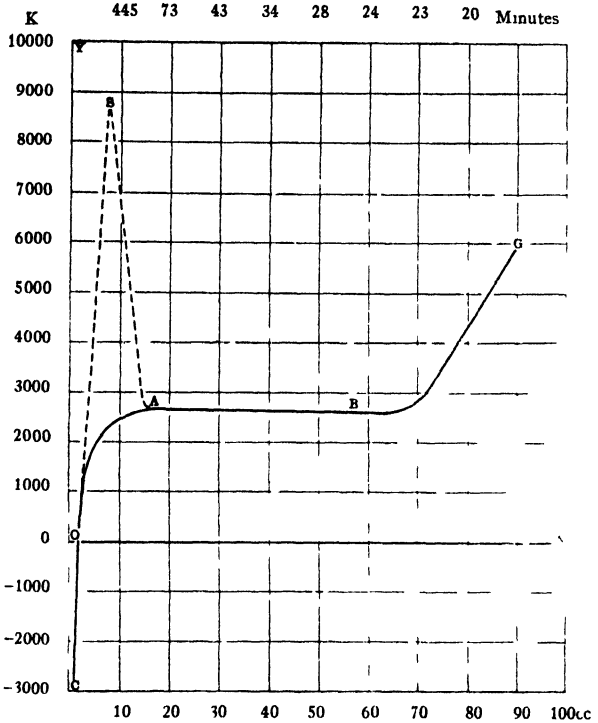


Figure 26 Ethyl alcohol Graph showing the variation of k Abscissa represents cc of alcohol per liter and ordinate represents cc. of alcohol per liter minus the theoretical threshold of toxicity concentration times survival time of the goldfish in minutes The portion AB is equivalent in range of concentration to AB of velocity of fatality curve Figure 17. $a=2.5$ cc. per liter $k=2625$. The activity of the goldfish represented by the dotted line has not yet been explained.

In Figure 24 the curve SPM=theoretical velocity of fatality curve of known LiCl solution, SP'M'=unknown solution No. 1, and SP''M''=unknown solution No. 2. 2.22 N.=normality of known LiCl solution. Then let v=normality of unknown solution No. 1 and u=unknown solution No. 2.

$$\text{Then } v : 2.22 : u = \frac{1}{OP'} : \frac{1}{OP} : \frac{1}{OP''} = \frac{1}{2.78} : \frac{1}{2.45} : \frac{1}{1.39} = 1.95 : 2{:}22 : 3{:}91.$$

Thus unknown solution No. 1=1.95 N. and No. 2=3:91.

For all methods suggested the temperature must be kept constant throughout the experiment and at the same temperature as that at which the standard theoretical velocity of fatality curve was prepared. These methods will not hold when the temperature varies.

Results which will allow the above interpretation have been derived independently by different workers (but not thus interpreted by them) in different groups of the animal kingdom as well as the plant kingdom. All will stand the above tests. Ostwald (1905) in his work on toxicity of sea-water and the constituents of sea-water on a fresh water isopod (*Gammarus pulex* De Geer) plotted survival time of the isopod as ordinate and proportion of sea-water or its constituents as abscissa. The curve thus formed when examined casually resembled an hyperbola, however he did not designate the curve as such, but stated, "I have not been able so far to figure out a formula that holds for the whole curve." Ostwald did not construct the reciprocal or velocity of fatality curve. When this curve is constructed from his data, (Table, page 72, showing survival times of male and female Gammarus in different proportions of sea-water, 1905) it resembles very closely the velocity of fatality curves shown in Figs. 1 to 20. Doubtless the resemblance would have been more striking had Ostwald tabulated his data which were omitted and had he run a few experiments with higher concentrations, as he states, "it was only from concentrations of 20 parts of fresh water with 80 parts sea-water and higher, that visible toxic effects began to appear. But these figures thus obtained were still so large and varied so much that I excluded them from my experiments." And later he says that the toxicity of all salts investigated increased very slowly at very low concentrations with increased concentration of solution depending on the nature of the salt and at stronger concentrations there was a sudden rise, while at still higher concentrations there was again a slow rise in toxicity. This is in complete accord with data obtained in this investigation. He then suggests that this difference in the rate of increase of the toxicity of a substance with increase in concentration at very low and at very high concentrations was due to the inability to measure very exactly the low concentrations and to inexactness in determining the death point in a very short survival period. Ostwald (1905, 1907) then disregards these extremes and applies to his mean data the absorption formula (Ostwald, 1906) $a=KC^m$ where $a=$ amount of salt absorbed, C=concentration of the solution, and K and m are constants depending on the nature of the salt investigated. He then assumes that the survival time of the Gammarus is inversely proportional to the amount of salt absorbed, i.e., $1/t=a$, thus $1/t=KC^m$ or $tC=K_1$. Later Ostwald (Ostwald and Dernoscheck, 1910) recognized the inability of the formula to fit his experimental data, and revised his formula by substituting $(C-n)$ for C where $n=$amount of the salt tested normally found in the blood of the experimental animal. But it is difficult to see why such a substitution should be made wih substances not normally found in the blood of the animal. This as has been pointed out would be necessary with all substances tested, since all undergo the same variation in toxic activity with variation in concentration as that pointed out by Ostwald. The only exceptions are $CuCl_2$,

$CdCl_2$, and $FeCl_3$. See page 35. Křiženecký (1916) in his work on *Enchytraeus humicultor*, a fresh water annelid, showed that the survival time of these worms in different concentrations of sea-water, when data is plotted as above, gives a similar curve. Křiženecký explained these results as well as the greater part of the toxic effect of the alkali and alkaline earth metals tested by him as being due to osmotic pressure. He then formulates a curve by tabulating results obtained by determining the time required for the worm to recover in ordinary tap-water after being placed in different concentrations of sea-water for one minute. He then states that both curves have the characteristics of curves of autocatalytic processes in that they fall within the province of the theory of the temporal properties of life processes proposed by Ostwald (1908). Loeb (1903) in summarizing his work on a marine Gammarus, states that, "if sea-water be diluted by the addition of distilled water the duration of life decreases at first only slightly in the decrease of the degree of dilution. But as soon as a dilution of ten times is reached an abrupt decrease in the duration of life takes place with further dilution. Whether the curve of the duration of life at this place is discontinued is not yet proven." Data obtained from the work of Loeb and Wasteneys (1913) on the reduction of oxidation of fertilized eggs of sea-urchins by the addition of .01% KCN solution to sea-water gives a similar curve when per cent of loss of rate of oxidation is plotted as ordinate and relative amount of KCN added to the sea-water as abscissa, Fig. 27. The per cent of reduction of the rate of oxidation of an individual sponge as given by Hyman (1916) in her work showing the effect of KCN on the reduction of the rate of consumption of oxygen by a marine sponge also gives a similar curve when per cent of reduction of oxygen consumption is plotted as ordinate and normality of KCN as abscissa (only data on a single

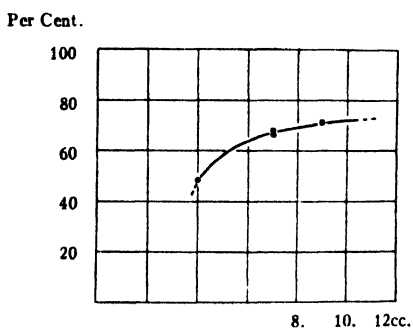


Figure 27. Curve showing the effect of potassium cyanide on the rate of oxygen absorption of fertilized eggs of the sea urchin. Abscissa represents cc. of 0.01% KCN per 50 cc. sea-water. Ordinate represents the per cent of reduction of rate of oxygen absorption below the normal by the potassium cyanide.

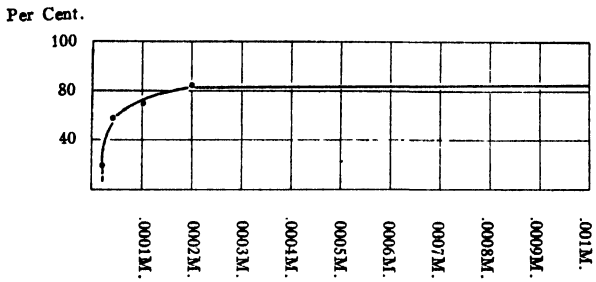


Figure 28. Curve showing the effect of potassium cyanide on the oxygen absorption of a marine sponge. Abscissa represents mols, per liter in sea water. Ordinate represents the per cent of the rate of oxygen absorption reduced by the potassium cyanide below the normal during a unit time (150 minutes). Data taken from Hyman (1916). All data taken from experiments on an individual sponge.

sponge were taken) Fig. 28. The last two calculations are not made on the same basis as the preceding curves but are sufficiently comparable to show that both probably follow the same general law as the toxic activity of salts. A curve formulated from data given in Experiment 1, of Pittenger and Vanderkleed's (1915) preliminary work on the goldfish as a test animal is shown in Fig. 29. This is the same type of curve. This work of Pittenger and Vander-

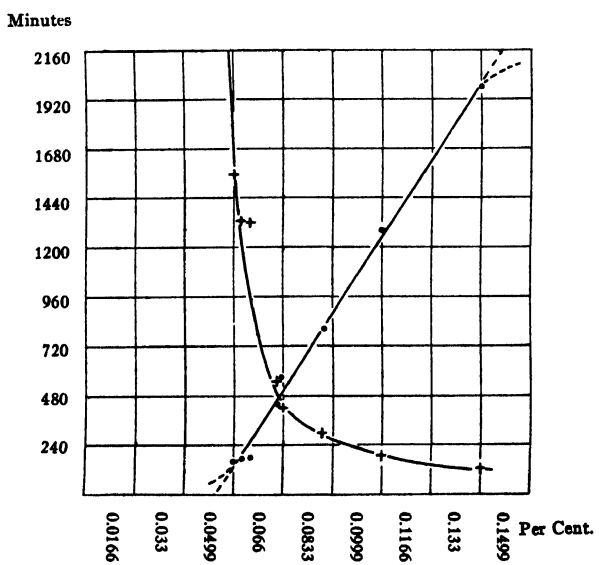


Figure 29. Digitalis. Velocity of fatality and survival time curves. Abscissa represents per cent concentration. Data taken from Pittenger and Vanderkleed (1915).

kleed has been very severely criticized. Many have questioned, as some have put it, "the smooth and elegant results." These smooth and elegant results obtained by these workers are due at least in part to the fact that they were working with solutions which fall within the portion of the velocity of fatality curve that approaches a straight line. (Compare to the portion A to B, curve CABG, Fig. 1.) While the concentrations with which their critics worked possibly fell outside this range of concentrations, it is probable that if their data be reviewed from this point of view it will become more intelligible.

From data obtained in this investigation it is clear that all experimentation for pharmacodynamic assay work should fall within the portion A to B of

TABLE XXXII

THE VARIATION OF THE SURVIVAL TIME OF GOLDFISH

0.318 N. MAGNESIUM CHLORIDE 21° C.		0.284 N. CALCIUM CHLORIDI 21° C.		0.274 N. STRONTIUM CHLORIDE 20.5° C.		0.214 N. BARIUM CHLORIDE 20° C.	
Weight of fish in grams	Survival time of fish in minutes	Weight of fish in grams	Survival time of fish in minutes	Weight of fish in grams	Survival time of fish in minutes	Weight of fish in grams	Survival time of fish in minutes
2.2	73	2.05	110*	2.95	96	1.9	86
2.3	74	2.3	145	2.2	85	2.2	85
2.4	41*	2.4	87*	2.25	73	2.2	89
2.4	75	2.4	95*	2.4	112*	2.3	94*
2.4	76	2.5	96	2.7	89	2.4	91
2.4	77	2.6	93*	2.85	99*	2.4	94*
2.5	78*	2.7	84*	2.9	101*	2.4	101
2.6	77*	3.3	100*	3.0	115*	2.5	100

*Fish was not dead when taken out of solution.

the velocity of fatality curve CABG, Fig. 1. The question then arises by what method can one determine with the least number of preliminary experiments the portion of the curve at which one is working. This can be done either by knowing the extremes of the survival time of the goldfish when the concentrations are within the designated range (A to B) or by running only three preliminary experiments at different concentrations. If the velocity of fatality curve formed by plotting the data from these experiments is convex with respect to the X-axis, the substance should be tested by using solutions falling near the weakest or between the two weaker solutions. If the curve is concave, solutions nearer the strongest or between the two stronger solutions should be used. If the curve is nearly straight and approaches a parallel position to the X-axis the solutions are either too weak or too strong. (These

seem to be the concentrations used by most pharmaceutical workers who have tested the goldfish method of Pittenger and Vanderkleed.) The time required to kill the goldfish will generally tell one whether the solutions are too strong or too weak. See discussion of survival time curve, page 48. If the curve approaches a straight line and is at an angle to the X-axis the solutions are of the most effective concentration. A second method consists in running only one experiment, determining the survival time of the goldfish, and applying this datum to the survival time curve (Curve LIJM, Fig. 1) or to the curve of the constant (Figs. 25 and 26) and reading directly the approximate concentration of the unknown. These curves also show the range of concentrations (concentrations represented by the portions of the curves A to B) most advantageous to use.

TABLE XXXIII
0.246 N. POTASSIUM CHLORIDE

Weight of fish in grams	Survival time of fish in minutes	Temperature Experiment Centigrade	Temperature Stock Centigrade
3.0	16	19.5°	19.5 to 22°
4.3	61	"	" " "
4.7	60	"	" " "
4.75	58	"	" " "
4.9	32	"	" " "
5.1	45	"	" " "
5.05	35	21°	20° " 21.5°
5.4	37	"	" " "
4.4	49	22°	15.5° " 16.5
4.4	79	"	" " "
4.7	42	"	" " "
6.4	69	"	" " "
3.9	46	16.5°	19.5° " 22°
4.9	37**	"	" " "
4.85	37	"	" " "
5.1	83	"	" " "
4.8	57*	"	15.5° " 16.5°
5.3	64	"	" " "
5.75	57	"	" " "
5.8	77	"	" " "

*Fish was not dead when taken out of the solution

**Fish was inactive and on side for about 1/2 minute or less immediately after being placed in solution

TABLE XXXIV
0.2223 POTASSIUM NITRATE

Weight of fish in grams	Survival time of fish in minutes	Temperature Experiment Centigrade	Temperature Stock Centigrade
3.4	31	19.5°	19° to 21°
3.4	35	"	" " "
6.1	70	"	" " "
3.9	45	"	15.5° " 16.5°
4.1	95	"	" " "
5.4	31	"	" " "
4.3	45	15.5°	19° " 21°
4.7	59	"	" " "
4.7	62	"	" " "
4.2	56	"	15.5° " 16.5°
4.8	70	"	" " "
5.1	46	"	" " "

TABLE XXXV
THE VARIATION OF SURVIVAL TIME OF GOLDFISH

Weight of fish in grams	Survival time of fish in minutes	Temperature Experiment	Weight of fish in grams	Survival time of fish in minutes	Temperature Experiment
.250 N. Magnesium Nitrate			.244 N. Magnesium Nitrate		
4.4	87	20°	4.7	40	19°
5.3	47	"	5.2	85	"
5.6	46	"	5.5	85	"
6.0	62	19°	5.5	48	"
6.0	79	"	5.6	45	"
6.1	42	"	5.6	128	"
6.3	59	20°	6.7	42	"
7.3	102	19°	7.1	57	"

SUMMARY OF CONCLUSIONS

1. The survival time of the goldfish (*Carassius carassius* L.) has a very definite relation to the concentration of the solution of the toxic substance used. This relation of the survival time of a goldfish to the concentration of the solution of the toxic substance follows a common general law with a very few exceptions which can be expressed as follows.

a. There is a concentration of each of the toxic substances tested which will just cause the death of a goldfish and concentrations below this will not cause death. This concentration has been designated as the threshold of toxicity concentration.

b. In concentrations of a toxic substance just above its threshold of toxicity concentration the velocity of fatality of the goldfish (as measured by the reciprocal of the survival time of the goldfish) is increased very slowly with increase in concentration of the solution of the toxic substance.

c. In stronger concentrations the velocity of fatality is increased more rapidly with the increase in the concentration of the solution.

d. And finally at very high concentrations the increase of velocity of fatality is again less rapid in proportion to the increase in concentration of the solution.

2. The survival time curve which is plotted by letting ordinate represent survival time of the goldfish and abscissa represent normality or the amount of substance used per l. of water is not an equilateral hyperbola but is logarithmic in function.

3. A curve, the velocity of fatality curve, which is formed by plotting the reciprocal of the survival time of the goldfish as ordinate and concentration of the solution as abscissa resembles a curve which can be expressed by $Y = \frac{1}{t} = \frac{K_2M + K_1X}{\log_e \left(\frac{M}{M-z} + \frac{K_2Mz}{K^1(M-z)} \cdot \frac{1}{X}\right)}$ M = normal rate of metabolism of a goldfish, z = loss of rate of metabolism of the goldfish when in a solution a toxic substance, Y = reciprocal of the survival time of the goldfish, and K_1 and K_2 = two constants depending on the nature of the metabolic process or processes involved and the nature of the toxic substance used.

4. The velocity of fatality curve approaches a straight line when the normality or amounts of toxic substance used per l. of water will not kill the goldfish in less than 45 minutes and does not require longer than 210 minutes. Data within these limits when survival time of the goldfish is plotted as ordinate and the concentration of the toxic substance as abscissa forms a curve which approaches an equilateral hyperbola and can be expressed for all practical purposes by the equation $y(x-a) = k$, where a = distance from the origin where

the portion of the velocity of fatality curve that approaches a straight line when prolonged cuts the X-axis and k=a constant. This straight line which is thus drawn has been designated as the theoretical velocity of toxicity curve. The concentration of the toxic substance represented by the point on the X-axis cut by the theoretical velocity of fatality curve has been designated as the theoretical threshold of toxicity concentration.

5. It has been suggested that relative toxicities of substances be expressed by the formula $T = \sqrt{\frac{\tan. \Theta}{a}}$ when only data which fall within the portion of the velocity of fatality curve which approaches a straight line are used. Θ=angle made by the theoretical velocity of fatality curve cutting the X-axis and a=the theoretical threshold of toxicity concentration of the substance tested. This expression does not represent either the absolute or the exact relative toxicities of the substances since it is based only upon the portion of the velocity of fatality curve which approaches a straight line, but has been chosen since it is a natural criterion and not an arbitrary one.

6. Four modifications of a definite survival time of the goldfish method of pharmacodynamic assay work as suggested by Pittenger and Vanderkleed have been proposed.

a. A definite survival time of the goldfish can be employed provided that the concentration of the substance to be tested is within the range of concentrations in which the velocity of fatality curve approaches a straight line.

b. The average survival time of a number of goldfish in a solution of the substance to be tested can be applied as ordinate to a standard survival time curve and the strength of the solution can be read directly from the abscissa provided this data falls within the limits of the survival time curve which approaches an equilateral hyperbola, i.e., where the velocity of fatality curve approaches a straight line.

c. The average survival time of a number of goldfish killed in a solution of the toxic substance to be tested can be substituted in the equation $y(x-a) = k$ and the value of x determined which will be the concentration of the solution of the substance tested, provided the survival time of the goldfish is within certain maximum and minimum of survival time, the reciprocals of which when plotted as ordinate and the concentrations of the solutions used as abscissa will approach a straight line, y=survival time of the goldfish, x=concentration of solution of the toxic substance in which the goldfish are killed, a=the theoretical threshold of toxicity concentration, and k=a constant depending upon the substance tested.

d. The average survival time of the goldfish killed in a solution of the substance to be tested can be applied to a graph which has been prepared to show the values of k in different concentrations of the substance with survival time interpolated at the top of graph and the concentration of the solution can be read directly from the abscissa. (See Figs. 25 and 26.)

7. A fifth method of pharmacodynamic testing has been suggested which consists of comparing the velocity of fatality curve of an unknown solution with that of a known solution of the same substance. The strengths of the solutions are inversely proportional to the number of cc. per l. of the original solutions or the number of grams per l. of the two substances required to make up a theoretical threshold of toxicity concentration of the substance.

8. A rise in temperature increases the toxic activity of a substance which probably follows the same general law as that of the activity of toxic substances. This has not been proven and needs further investigation.

BIBLIOGRAPHY

ALLEE, W. C.
1916. Chemical Control of Rheotaxis in Asellus. Jour. Exp. Zool., 21:163-198.
BAKER, W. F.
1913. How Far Variations in Frogs can be Obviated by the Use of Ouabain. Lilly Sci. Bull., ser. 1, no. 3, pp. 71-79.
BERNARD, C.
1857. Leçons sur les effets des substances toxiques et médicamenteuses. Paris.
BERT, P.
1871. Sur les phénomènes et les causes de la mort des animaux d'eau douce que l'on plonge dans l'eau de mer. Compt. rend. acad. sci., 73:382-385; 464-467.
BINET, P.
1892. Physiologie Experimentale. Sur la toxicité comparée des métaux alcalins et alcalino-terraux. Compt. rend. acad. sci., 115:251-253.
BLAKE, J.
1883. On the Connection between Physiological Action and Chemical Constitution. Jour. Physiol., 5:35-44.
1887. Relation of the Chemical Constitution of Inorganic Compounds to their Physiological Action. Chem. News, 55:110-111.
BOTKIN, S.
1885. Zur Frage über den Zusammenhang der physiologischen Wirkung mit den chemischen Eigenschaften der Alkalimetalle der ersten Gruppe nach Mendelejeffe. Centr. albl med. Wissensch., 23:848.
BULLOT, G.
1904. On the Toxicity of Distilled Water for the Fresh Water Gammarus. Suppression of This Toxicity by the Addition of Small Quantities of Sodium Chloride. Univ. Cal. Publ. Physiol., 1:199-217.
BURGE, W. E.
1917. Why Chloroform is a More Powerful and Dangerous Anesthetic than Ether. Science, n.s., 46:618-620.
BURGE, W E. and BURGE, E. L.
1914. The Rôle of Nascent Oxygen in Regulating the Activities of Enzymes in Animals and Plants. Amer. Jour. Physiol., 34:140-148.
1915. The Protection of Parasites in the Digestive Tract against the Actions of the Digestive Enzymes. Jour. Parasit., 1:179-183.
CHILD, C. M.
1915. Senesence and Rejuvenescence. Chicago.
CLARK, J. F.
1899. On the Toxic Effect of Deleterious Agents on the Germination and Development of Certain Filamentous Fungi. Bot. Gaz., 28:289-327.
CLAYBERG, H. D.
1917. The Effect of Ether and Chloroform on Certain Fishes. Biol. Bull., 32:234-248.
DRIESCH, H.
1909. The Science and Philosophy of the Organism. London.
FAGGE, C. H. and STEVENSON, T.
1866. On the Application of Physiological Tests for Certain Organic Poisons and Especially Digitaline. Guy's Hospital Rep. Lond., 12:37.
GARREY, W. E.
1905. The Osmotic Pressure of Sea-water and the Blood of Marine Animals. Biol. Bull., 8:257-270.

1915. The Resistance of Fish to Changes of Osmotic Pressure and Chemical Conditions. Amer. Jour. Physiol., 39:313-329.

GEPPERT, J.

1889. Ueber des Wesen der Blausäurevergiftung. Zeit. klin. Med., 15:208-242, 307-369.

GREGERSEN, J. P.

1916. Untersuchungen über die antiseptische Wirkung des Magensaftes. Centr. Bakt. Par., Orig., 77:353-361.

GUNN, J. W C.

1914. The Influence of Temperature on the Action of Strophantin on the Mammalian Heart., Jour. Pharm. Exp. Ther., 6:39-44.

HASKELL, C. C.

1913. The Influence of Temperature on the Results Secured by Houghton's Method of Assay for the Heart Tonics. Lilly Sci. Bull., ser. 1, no. 5, pp. 199-201.

1914. The Physiological Activity of Ergotin and Powdered Extracts of Ergot. Jour. Amer. Pharm. Assn., 3:786.

HATCHER, R. A. and BRODY, J. G.

1910. Biological Standardization of Drugs. Amer. Jour. Pharm., 82:360-372.

HEFFTER, A.

1908. Giebt es reduzierende Fermente im Tierkörper? Arch. exp. Path., Suppl., 59:253-260.

HOPKINS, F. G.

1914. The Dynamic Side of Biochemistry. Report Brit. Assn. Adv. Sci., Birmingham, 1913; 652-668.

HOUGHTON, E. M.

1898. Pharmacologic Assay of the Heart Tonics. Jour. Amer. Med. Assn., 31:959-961.

HYMAN, L. H.

1916. On the Action of Certain Substances on Oxygen Consumption. I. The Action of Potassium Cyanide. Amer. Jour. Physiol., 40:238-248.

JOSEPH, D. R. and MELTZER, S. J.

1909. The Comparative Toxicity of the Chlorides of Magnesium, Calcium, Potassium and Sodium. Jour. Pharm. Exp. Ther., 1:1-26.

KAHLENBERG, L, and AUSTIN, R. M.

1900. On the Toxic Action of Acid Sodium Salts on *Lupinus albus*. Jour. Phys. Chem., 4:553-569.

KAHLENBERG, L. and MEHL, H. F.

1901. Toxic Action of Electolytes upon Fishes. Jour. Phys. Chem., 5:113-132.

KAHLENBERG, L. and TRUE, R. H.

1896. On the Toxic Action of Dissolved Salts and their Electrolytic Dissociation. Bot. Gaz., 22:81-124.

KASTLE, J. H. and LOEVENHART, A. S.

1901. On the Nature of Certain of the Oxidizing Ferments. Amer. Chem. Jour., 26:539-566.

KISSKALT, K.

1915. Über die Beziehungen der tödlichen Dosis zur Oberfläche. Biochem. Zeit., 71:468-478.

KŘIŽENECKÝ, J.

1916. Ein Beitrag zum Studium der Bedeutung osmotischer Verhältnisse des Medium für Organismen. Arch. ges. Physiol., 163:325-354.

KROGH, A.

1914. On the Influence of the Temperature on the Rate of Embryonic Development. Zeit. allgem. Physiol., 16:163-177.

1914a. On the Rate of Development and CO_2 Production of Chrysalides of *Tenebrio molitor* at Different Temperatures. Zeit. allgem. Physiol., 16:178-190.

LABORDE, J. V.
1884. Sur le mécanisme de la mort ou des accidents qui succèdent a l'injection sous-cutanée du chloroforme, à propos d'une Note de M. Bouchard sur le même sujet. Compt. rend. soc. biol., 36:271-278.
LILLIE, R. S.
1902. On the Oxidative Properties of the Cell-nucleus. Amer. Jour. Physiol., 7:412-321.
LOCKE, F. S.
1895. On a Supposed Action of Distilled Water as Such on Certain Animal Organisms. Jour. Physiol., 18:319-331.
LODGE, O.
1913. Continuity. Science, n. s., 38:379-395, 417-430.
LOEB, J.
1902. Studies on the Physiological Effect of Valency and Possibly the Electrical Charges of the Ions. I. The Toxic and Anti-toxic Effects of Ions as a Function of the Valency and Possibly their Electrical Charge. Amer. Jour. Physiol., 6:411-433.
1903. On the Relative Toxicity of Distilled Water, Sugar Solutions and Solutions of the Various Constituents of Sea-water for Marine Animals. Univ. Cal. Publ., Physiol., 1:55-69.
LOEB, J. and WASTENEYS, H.
1913. Is Narcosis due to Asphyxiation? Jour. Biol. Chem., 14:517-523.
LOEVENHART, A. S. and KASTLE, J. H.
1903. On the Catalytic Decomposition of Hydrogen Peroxide and the Mechanism of Induced Oxidations. Together with a Note on the Nature and Function of Catalase. Pt. I. Amer. Chem. Jour., 29:397-437.
MATHEWS, A. P.
1903. The Nature of Nerve Irritability, and of Chemical and Electrical Stimulation. Pt. II. Science, n.s., 17:729-733.
1904. The Relation between Solution Tension, Atomic Volume and the physiological Action of the Elements. Amer. Jour. Physiol., 10:290-323.
1907. The Cause of the Pharmacological Action of Ammonium Salts. Amer. Jour. Physiol., 18:58-63.
1916. Physiological Chemistry. New York.
MATHEWS, A. P. and WALKER, S.
1909. The Action of Cyanides and Nitriles on the Spontaneous Oxidation of Cystein. Jour. Biol. Chem., 6:29-37.
MEEK, S. E. and HILDERBRAND, S. F.
1910. A Synoptic List of the Fishes Known to Occur within 50 Miles of Chicago. Field Mus. Nat. Hist. Publ., Zoology, 7:223-338.
MIYAKE, K.
1916. The Toxic Action of the Soluble Aluminum Salts upon the Growth of the Rice Plant. Jour. Biol. Chem., 25:23-28.
MOORE, W.
1917. Toxicity of Various Benzene Derivatives to Insects. Jour. Agr. Res., 9:371-381.
MOORE, W. and MOORE, J. J.
1917. Studies in Greenhouse Fumigation with Hydrocyanic Acid: Physiological Effects on the Plant. Jour. Agr. Res., 11:319-338.
OSTERHOUT, W. J. V.
1915. The Measurement of Toxicity. Jour. Biol. Chem., 23:67-70.
OSTWALD, W.
1906. Lehrbuch der allgemeinen Chemie, 2 Bd. Leipzig.
OSTWALD, W.
1905. Studies on the Toxicity of the Sea-water for Fresh Water Animals (*Gammarus pulex* De Geer). Univ. Cal. Publ. Physiol., 2:163-191.

1907. Über die Beziehungen zwischen Adsorption und Giftigkeit von Salzlösungen für Süsswassertiere (Gammarus). Arch. ges. Physiol., 120:19-30.
1908. Über die zeitlichen Eigenschaften der Entwicklungsvorgänge. Vortr. Aufsät. Entwicklungsm., Heft 5.

OSTWALD, W. and DERNOSCHECK, A.
1910. Ueber die Beziehungen zwischen Adsorption und Giftigkeit. Zeit. Chem. Ind. Kolloide, 6:297-307.

PAULI, W.
1903. Untersuchungen über physikalische Zustandsänderungen der Kolloide. Beitr. chem. Physiol. Path., 3:225-246.

PITTENGER, P. S. and VANDERKLEED, C. E.
1915. Preliminary Notes on a new Pharmacodynamic Assay Method. Jour. Amer. Pharm. Assn., 4:427-433.

REED, E. D. and VANDERKLEED, C. E.
1908. The Standardization of Preparations of Digitalis by Physiological and Chemical Means. Amer. Jour. Pharm., 80:110-120.

REIBISCH, J.
1902. Ueber den Einfluss der Temperatur auf die Entwicklung von Fisch-Eiern. Wiss. Meersuntersuch. Kiel., N. F., 6:215-231.

RICHARDS, A. N. and WALLACE, G. B.
1908. The Influence of Potassium Cyanide upon Proteid Metabolism. Jour. Biol. Chem., 4:179-195.

RICHET, C.
1881. De la toxicité comparée des différents métaux. Compt. rend. acad. sci., 93:649-651.

RINGER, S.
1882. An Investigation Regarding the Action of Rubidium and Caesium Salts Compared with the Action of Potash Salts on the Ventricle of the Frog's Heart. Jour. Physiol., 4:370-379.
1883. Concerning the Influence of Saline Media on Fish etc. Jour. Physiol., 5:98-115.
1897. The Action of Distilled Water on Tubifex. Jour. Physiol., 22:xiv-xv (Proc).

ROBERTSON, T. B.
1908. On the Normal Rate of Growth of an Individual, and its Biochemical Significance. Arch. Entwickl. Organ., 25:581-614.

ROBIN, A.
1914. Colloidal Sulphur. Répert. Pharm. 70:161-162 (Cited from Chem. Abst., p. 2920.)

SANDERSON, E. D. and PEAIRS, L. M.
1913. The Relation of Temperature to Insect Life. Tech. Bull. N. H. Coll. Ag. Exp. Sta., 7:1-125.

SHAFER, G. D.
1915. How Contact Insecticides Kill. III. Tech. Bull. Mich. Agr. Coll. Sta., 21:1-67.

SHELFORD, V. E.
1917. An Experimental Study of the Effects of Gas Waste upon Fishes, with Special Reference to Stream Pollution. Bull. Ill. State Lab. Nat. Hist., 11:381-412.
1918. Physiological Problems in the Life Histories of Animals with particular Reference to their Seasonal Appearance. Amer. Nat., 52:129-154.

SOLLMANN, T., MENDENHALL, W. L. and STINGEL, J. L.
1915. The Influence of Temperature and Concentration on the Quantitative Reaction of the Heart to Ouabain. Jour. Pharm., 6:533-560.

TOWNSEND, C. O.
1901. The Effect of Hydrocyanic-acid Gas upon Grains and Other Seeds. Bull. Md. Agr. Exp. Sta., 75:183-198.

TROLAND, L. T.
1917. Biological Enigmas and the Theory of Enzyme Action. Amer. Nat., 51:321-350.
VERWORN, M.
1909. Allgemeine Physiologie. Jena.
WARREN, E.
1900. On the Reaction of *Daphnia magna* (Straus) to Certain Changes in its Environment Quart. Jour. Micr. Sci., 43:199-224.
WELLS, M. M.
1914. Resistance and Reactions of Fishes to Temperature. Trans. Ill. State Acad. Sci., 7:48-59.
1915. Reactions and Resistance of Fishes in their Natural Environment to Acidity, Alkalinity and Neutrality. Biol. Bull., 29:221-257.
WOODWORTH, C. W.
1915. The Toxicity of Insecticides. Science, n.s., 41:367-369.
ZIEGER, R.
1915. Zur Kenntnis der Katalase der niederen Tiere. Biochem. Zeit., 69:39-110.

ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. IV January, 1918 No. 3

EDITORIAL COMMITTEE

STEPHEN ALFRED FORBES WILLIAM TRELEASE

HENRY BALDWIN WARD

PUBLISHED UNDER THE
AUSPICES OF THE GRADUATE SCHOOL BY
THE UNIVERSITY OF ILLINOIS

COPYRIGHT, 1918 BY THE UNIVERSITY OF ILLINOIS
DISTRIBUTED DECEMBER 31, 1918

MORPHOLOGY AND BIOLOGY OF SOME TURBELLARIA FROM THE MISSISSIPPI BASIN

WITH THREE PLATES

BY

RUTH HIGLEY

Contributions from the
Zoological Laboratory of the University of Illinois
Under the Direction of Henry B. Ward, No. 112

THESIS

SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY IN ZOOLOGY IN THE GRADUATE

SCHOOL OF THE UNIVERSITY OF ILLINOIS

1917

TABLE OF CONTENTS

	PAGE
Introduction	7
Technique	9
Methods of Study	10
Biology	12
Types of Localities	12
Reactions of Worms	17
Morphology	22
Family Planariidae	22
Planaria velata Stringer 1909	22
Planaria maculata Leidy 1847	23
Planaria truncata Leidy 1851	24
Family Catenulidae	25
Stenostoma leucops (Ant. Dugès) 1828	26
Stenostoma tenuicauda von Graff 1911	30
Stenostoma giganteum nov. spec.	30
Stenostoma glandiferum nov. spec.	35
Family Microstomidae	37
Microstoma caudatum Leidy 1852	38
Macrostoma sensitivum Silliman 1884	39
Macrostoma album nov. spec.	39
Family Prorhynchidae	42
Prorhynchus stagnalis M. Schultze 1851	43
Prorhynchus applanatus Kennel 1888	44
Family Dalyelliidae	45
Dalyellia dodgei von Graff 1911	46
Dalyellia alba nov. spec.	47
Dalyellia megacephala nov. spec.	49
Family Typhloplanidae	50
Rhynchomesostoma rostratum (Müller) 1774	51
Strongylostoma rosaceum nov. spec.	52
Epithelium	54
Muscular system	57
Parenchyma	58
Digestive System	59
Nervous System	60
Excretory System	62
Reproductive System	63
Development	64
Life Habits	69
Typhloplana viridata (Abildgaard) 1789	71
Mesostoma ehrenbergii (Focke) 1836	73

Mesostoma angulare nov. spec. 74
Mesostoma simplex nov. spec. 77

Family Gyratricidae 78
Gyratrix hermaphroditus Ehrenberg 1831 78

Conclusions and Summary 81
General discussion 81
Summary 84

Bibliography 85

Explanation of Plates 88

INTRODUCTION

Although commonly little known, the Turbellaria as a class present certain characters of morphology and life-history which make them of especial interest. Furthermore, their biologic processes and life habits in relation to other forms, shed some light upon general problems of common existence. A knowledge of any group of animals is of value from a phylogenetic standpoint and also in the explanation of the interdependence among various types. So a study of this group, which stands out as a connection between the very lowest phyla, the aberrant parasitic worms, and the more specialized higher types, makes possible an understanding of one of the steps in the evolution of the animal kingdom, namely the transition from radial to bilateral symmetry. The simplicity of anatomical structure and lack of conspicuous detail, thus especially important in a comparative way, also enable these forms to carry on an existence almost unsuspected and generally entirely overlooked. The fact of their widespread distribution in both salt and fresh water passes, for the most part, unnoticed.

While the fresh water Turbellaria of Europe have been recognized and carefully studied for nearly one hundred and fifty years, the American species have received little attention. The earliest records for this country are those of Leidy. In 1848, he gave the first brief description of the now well-known and very common *Planaria maculata*. He also studied rather completely *Phagocata gracilis*, distinguishing the fundamental points in which it differed from Planaria. Later (1852) he added several other species to the list. No other studies were reported until a paper by Silliman appeared in 1885. This was also descriptive and systematic in character. The first morphological work was that by Ott (1892) who made the common *Stenostoma leucops* O. Sch. the basis of a detailed histological study. Woodworth (1896, 1897) next published results of collections made from rather widely separated localities, viz., Massachusetts and Illinois. He named four new species and added full descriptions of twelve others.

Since 1900 there have appeared a number of papers, a few descriptive, but by far the most the results of experimental work. Of the first type, the paper by von Graff (1911) is noteworthy. In this, he gives descriptions and notes of some seventy-five species. Several other writers have from time to time added a few forms, but this is all. On the other hand, the more common species have been used in a vast amount of experimental work. Child's work with the common flatworm has explained a large number of facts of far-reaching general biologic significance. Other investigations, some of them exhaustive, have dealt with the more primitive rhabdocoels as well as with planarians. Among the many writers along this line are Kepner (1911, 1915), Curtis (1905), and Pearl (1903).

Although in general the Turbellaria are free-living forms, a few cases have been reported in which they are parasitic on molluscs and it is in these species that a beginning has been made in the study of the embryology and life-history. Two writers, Linton (1910) and Stanley C. Ball (1916), have published such investigations of a species living on Modiolus.

The Turbellaria of the central and western states are almost unknown. Woodworth (1897) and Stringer (1909, 1913) have published descriptions of five new species from Illinois and Nebraska. Eleven other forms, found also in the eastern states, have been reported from a few localities in Illinois, Nebraska, Michigan, and Wisconsin, but these are all. That some species, at least, are present in great numbers is evident from the various collections for experimental studies. The whole Mississippi valley region with its lakes and almost numberless ponds furnishes conditions in many respects ideal for such types, and their existence will sooner or later be demonstrated.

In fact, both Planaria and Rhabdocoelida are of much more common occurrence than is generally supposed and for several reasons are especially valuable for study. First, they are available as living reproducing animals thruout the year. Then, they are good for experimental work since they illustrate a somewhat primitive phylum, one in which the body structure is very different from that commonly encountered. Well adapted to such studies by their simplicity and great vitality, they have come to be the classic specimens employed both for elementary experiment and for complicated investigation. The free-living method of life, together with the simple fundamental anatomy, when compared with the specialized and much changed condition of the nearly related parasitic worms, shows clearly the variations possible and actually brought about by a different mode of life. As a whole, the group is of more than ordinary interest.

Always considered of no importance economically, their possible relation to other forms has been overlooked, so that only by chance have their habits of parasitism and voracious feeding been discovered, and there is need of further investigation along this line.

In the present paper is reported a brief study of a few forms found in small lakes and ponds in Illinois and Iowa. This work covers three phases: First, a summary and comparison of the types of habitat which deals with such environmental factors as flora, whether algae or higher water plants, animal communities, whether few or many, bottom, whether sandy or muddy, and also the general water conditions; second, a few of the biological aspects, this outline comprising a study of the reactions to the various stimuli; third, a morphological description of eight new species and additional data concerning fifteen others. These descriptions embrace to some extent histological structure as well as gross anatomy, and a number of points regarding the distribution and characteristic variations of well-known species. In the case of one form a brief résumé of the embryological stages is also given. In the plates are included, toto drawings of all the species, besides separate sketches of isolated parts.

The work, which was carried on for the most part at the University of Illinois, was undertaken at the suggestion of Dr. Henry B. Ward. To him I wish to express my sincere gratitude and appreciation for special opportunities and for his great help and inspiration.

I also had the opportunity to make collections and to study at the United States Biological Station at Fairport, Iowa, and my thanks are due to the director, Mr. A. F. Shira, and to Mr. H. L. Canfield, who aided me in every way possible. I am also indebted to Mr. R. L. Barney, of the United States Biological Station at Homer, Minnesota, for material sent me, and to Miss Elizabeth Bodfish, of the University of Illinois, for many specimens from Urbana localities.

Through the kindness of Dr. Stephen A. Forbes, director of the Illinois State Laboratory of Natural History, I was able to learn something of the conditions along the Illinois river at Havana and at Cedar Lake, having at my command the facilities of the laboratory. I wish to express my deep appreciation of these privileges.

TECHNIQUE

Collections were made in three ways. Surfaces or open water was dipped up with a pail or jar, and as large amounts as possible carried back to the laboratory, partly for the purpose of ascertaining whether or not specimens were present, and partly for use in aquaria. Then with a long-handled dip net, masses of algae and water-weed were taken either from shallow places along the shore line, or from the surface out in deeper water where they float in great tangles, or from the bottom. In some cases a good deal of water was drained off and the mass of damp weed carried in, to be later plunged in pond or tap water. As a third method, a mass of the alga was taken with a minimum of disturbance and kept as nearly as possible in its relative shape and condition. In small ponds where the water was not over three feet in depth, collections were made out in the middle and often the leaves and stems of water lilies and other large plants were gathered. These were kept by themselves in clear water. The stems and undersides of the lily pads were generally covered with very fine algae or a growth of diatoms, which made good shelter and feeding ground for many small forms. The bottom mud with its loose covering of organic debris was generally dipped up separately with a small amount of water. Samples were taken both near shore and out in the deeper portions.

Many collections were kept alive in the laboratory for lengths of time varying from a few days to six months. The algae and other debris were floated out in tap water, rain water, or pond water. Glass jars were used for this purpose, some very shallow and some eighteen inches deep. In cases where a few individuals or a special bit of water weed was to be isolated, shallow glass stender dishes were employed. About half the aquaria were kept covered to prevent evaporation and the others left open, water being added at

intervals. Varied amounts of sunlight were used. A few jars were placed so as to have sun all day but most had it for only a few hours at a time and a good many not at all. Generally the temperature of the aquaria was that of the room; a few however were held at a much higher and a few at a much lower point. Balanced and favorable conditions are always easy to obtain, and in a number of cases there was a good deal of asexual reproduction by budding, as a result of fairly perfect metabolism. Occasionally when a number of surrounding details were precisely favorable, even the sexual reproduction could be studied and the life habits made out with some degree of completeness.

The aquaria were never artificially aërated, but an attempt was always made to furnish oxygen by means of plant life. In the case of Planaria food was provided in the shape of small bits of meat, while in the jars where rhabdocoels were living there was always an abundance of other animal forms to supply all possible needs.

In preparation for histological study the specimens were killed and fixed with some measure of success. The individuals in some cases were anaesthetized with a solution of cocaine hydrochlorate followed by chloretone of varying strengths until they were quiet and expanded. The fixation was done with corrosive acetic solution. Material was generally stained in toto with Ehrlich's hematoxylin, embedded in paraffin, and sectioned 4 to 8μ in thickness. A counterstain of eosin or erythrosin was sometimes used. With Planaria a solution of one part nitric to three of water gave good results as a killing fluid. Cold corrosive sublimate was found useful in many instances, and under special conditions a warm solution was valuable.

METHODS OF STUDY

Specimens were studied either alive or in permanent mounts. When living they were controlled by means of a pipette and were isolated either in concave watch glasses or on a slide. The movements could be checked by burying in a drop of quince-seed jelly or by adding small amounts of cocaine or chloretone to the water. The jelly is of value in studying the cilia or the muscular system, for it increases the violence of action while retarding the speed. It also shows more clearly the relative position of various organs, for the animal will turn over again and again, thus affording good lateral and ventral views. The objection to its use lies in the fact that only a very thick, opaque solution will be dense enough to reduce the movement appreciably. The chloretone has the advantage of quieting the worm thoroly, but it also causes the specimen to become so limp as to be easily injured, and to begin to disintegrate very soon. Another way is to confine the animal by the weight of the cover glass or by using a minimum amount of water on the slide. This method flattens the body so as to make it more transparent, and also pushes the several organs entirely out of their natural position. But organs can be studied in this way better than under any other conditions, since they can be partially isolated and their interrelationships made out. Because of the transparency and lack of

rigidity, many details are clearer in the live tissue than in permanently mounted material, where a large amount of cellular contraction is unavoidable. Many details of structure, however, especially those of the nervous system, are clear only from a study of prepared material. Serial sections in the several planes have been used to verify and correlate findings in the various body systems.

Some little difficulty was experienced in an attempt to make a detailed study of the tissues. Their extreme contractility and sensitiveness make it almost impossible to kill and fix material in a condition anywhere near the normal. The delicacy of the structure as a whole as well as of every part, very much increases the chance of injury and even when great care is used, the tissues are generally somewhat torn and distorted. The integument is so easily ruptured that often only the weakest anesthetizing fluids can be used, and then complete quiet is not obtained. Then also the species which reproduce by budding break very easily at the line of division and are likely to be mutilated. As a consequence of this, especial gentleness and care must be used in the handling and control of all specimens.

BIOLOGY

TYPES OF LOCALITIES

During the past three years collections have been made in some eighty streams and ponds. The territory thus covered comprises several regions: in Illinois, the vicinity of Urbana and Havana in the central part, and at Cedar Lake in the north; in Iowa, regions near Fairport and Grandview along the Mississippi river and near Grinnell in the central part of the state; in Minnesota, at Homer which is in the south eastern corner; in Wisconsin, at Milwaukee. About fifty places have been visited only once, a number of others two or three times, while from a few, collections were made every few days for several months. The immediate surroundings, the state of the weather, the condition of the water, all varied to a greater or less degree. There were gradations from a sandy barren flat to a wooded hillside, from a hot July day to the intense cold of mid-winter with ice five feet in thickness, from a few quarts of thick muddy water to a stream the size of the Mississippi. The types of places investigated may be summarized as streams, ponds, springs, and temporary mudholes.

Springs and puddles seem to be unfavorable for many of the smaller animal forms, except in a few instances. In one place where the location made it possible and where the spring furnished sufficient water to make a fairly permanent little pond, both the plant and animal forms had a chance to develop and were present in abundance. Here Stenostoma was found in great numbers.

If puddles are made by the overflow from some stream or larger pond, then the plant and animal forms present will be those of the main supply which have become marooned. They will eke out an existence as long as conditions permit, or will thrive if chance favors them. Thus in some years the rains are not so heavy as to stir up a pond violently, and then if the situation is partly protected from the drying power of the sun the imprisoned fauna and flora may flourish thruout the season. If the water remains for some length of time so that filamentous algae have a chance to develop, there will probably be also many small crustaceans and an abundance of other life but no rhabdocoels. That is, species capable of finding transportation thru the air may gain a foothold in ponds where other species unable to do this will not. This, perhaps, explains first the presence of certain rhabdocoels in some mudholdes and not in others of different origin yet alike in general condition, and second their presence at one time and not at another.

The running water of streams and rivers does not produce situations favorable to delicate free-swimming organisms. Thus the type of turbellarian found in such places will be one able to find a sheltered and protected spot where there is also food and oxygen. At Milan, Illinois, where the Rock river flows over six or eight miles of rocky bed, planarians have an ideal location. Numbers of specimens are found clinging to the under side of nearly all the stones

which project up from the bottom or out into the water or which lie against each other so that the under side is not buried. The stones are more or less rough, covered with tiny crevices which make good hiding places, the worm being almost below the surface and thoroly protected but still able to make use of the swift current of fresh water. Collections were made in several other localities upstream and within the limits of the rocky bed, but no planarians were discovered.

A situation similar to the above is found in the Salt Fork of the Vermilion river at Homer, Illinois, where for a distance of a few hundred yards there are many rocks and stones in the stream bed. The water runs sluggishly everywhere except at one point, and here there is always a swift current from the overflow of a dam. This is an ideal locality and living upon the rocks over which the water is continually pouring are many planarians, the only ones to be found either up or down stream. The Sangamon is another stream of this same type, generally slow-flowing with few or no stones. Scattered planarians were found clinging to rocks at one place where a little fall gave rise to a swifter current for a short distance.

The larger rivers in this region with sandy or muddy bottom have, as a rule, a fairly even shore-line with few small coves or indentations, while a strong current generally keeps the banks washed clean of any driftwood or riff-raff which might lodge masses of organic debris and thus offer shelter to microscopic forms. On the side of the river where the current is undermining and changing the shore, no life of any sort is possible, but on the beach side, many clams, snails, and insect larvae find a feeding ground. These, however, are able to anchor themselves firmly in sand, while such types as flatworms and small crustaceans cannot exist. Altho there have been at different times many collections made by various workers and at numerous points along the Mississippi, rhabdocoels and planarians have not been reported. This absence seems to be easily explained since the conditions in the river are very different from those of any of its tributaries. Forms carrying on a thriving existence a few yards up some smaller stream meet with entirely new enemies in the main river and encounter there a powerful current which quickly tears them away as soon as they enter this expanse of water.

In the main branches of the Iowa a like situation prevails, but here all along the course there are numerous small ponds left by its periodic overflow. This backwater is generally protected by growths of willow and swamp maple, and may receive enough drainage from surrounding fields to last thruout the season. The plant and animal life is often very profuse and many Stenostoma species have been taken at different times from such ponds.

Another type of stream which often becomes a suitable location for many microscopic species as well as larger forms, is the artificial ditch or canal. Here the water generally flows slowly and comparatively evenly, there is little danger of flood, and many types gain a foothold. The Hennepin canal presents conditions rather unique in these respects. The banks are riff-raffed with rough

stones which make numerous crevices, the shore line is perfectly straight with never a break or an eddy to disturb the calm. There is movement sufficient to prevent the water from becoming stagnant but not sufficient to cause disturbance. The stones are covered with fine algae, thus forming an ideal feeding ground. The larger crustaceans, predacious larvae, and even most of the microscopic species find it a poor situation, so that the rhabdocoel enjoys an existence singularly free from enemies, tho on this same account the food supply is limited almost entirely to protozoa. Altho not plentiful in numbers, rhabdocoels are seemingly in control at least along the edge.

The most nearly ideal conditions for rhabdocoel existence are those found found in permanent ponds. Here the water is comparatively quiet, the plant life abundant and the small animal forms many. The hunting grounds for the small worm are sufficiently rich and the enemies so few that the problems of food supply and protection are almost nil.

In one such pond eight collections were made at intervals of from three to nine days, with essentially the same conditions and forms appearing each time. This was formerly a little stream racing thru an open valley protected by low hills on either side. The water is now held back by an earthen dam to make a pool about thirty yards across, with a depth of two and one half feet in the middle. It is kept stirred into a thick muddy semifluid by the wading cattle, and consequently there is little life of any sort. In direct contrast to this, below the dam for four hundred yards the water is clear, kept fresh by a little trickle coming through the spillway, and filled with an abundance of animal and plant life. Early in the summer it spreads out for one hundred yards with a depth of three feet, but later shrinks to one-half this size. The ground around is "mucky," covered thruout the marshy portion with swale; outside there is a region of Carex and Juncus. These, in the first place by their rigidity and harshness serve to keep away disturbing cattle, secondly, act as a windbreak so that not even a ripple disturbs the surface of the pond. The water is more or less filled with masses of Nostoc, Spirogyra, and diatoms. The number of protozoa is very large; then, of larger types, as water beetles, dragon flies, snails, frogs, etc., there is no lack. Members of the genus Stenostoma are abundant everywhere in water from the surface where they swim freely, from deeper more or less muddy portions, and clinging to water weed which yields great numbers even when transported in a thoroly drained condition. Out in the middle deeper portion are large patches of Nitella, which is nearly covered with organic debris and harbors many specimens. Some half-dozen species were secured, taken from different portions of the pond.

Another pool where many rhabdocoel species thrived, is in all respects a marked contrast to the above. This is Beatty Lake, a little body of water unique in its surroundings and formation. It is situated at about the level of the Mississippi river, not more than five hundred yards back from the shore line and with the ground between not more than six or eight feet high. The lake is bounded on the side away from the river by a mound seventy-five

feet in height which bends around to the southward, forming a nearly perpendicular wall. Toward the north, the sand slopes away gradually. Surrounded on all sides by barren sand, the pond is essentially a 'hole' with the bottom so near the river level that the water never seeps away, and with enough draining in to prevent its drying up completely, On the west and south the wind is entirely shut off, while even on the north and east the ground is high enough to prevent much of a ripple ever disturbing the surface from that direction. There is almost no vegetation within a hundred yards of the pond in any direction. This is partly due to the blowing of the sand which covers everything. In one place bush-like branches can be seen, all that remains unburied of three tall locust trees. The pond bottom is sandy, very solid, and smooth thruout. The banks slope very gradually into the water, which is quite clear, from two to five feet deep, very warm at the surface and cold two feet down. Tho used by cattle to some extent for drinking, the sand, when stirred up, quickly settles, leaving the water as clear as ever. There are no rushes, or other plants of this type, which reach up above the surface of the pond, so that the broad expanse is uninterrupted. Near the shallow portions within the pond, are great masses of very coarse Spirogyra, showing a brilliant green against the sandy background. There are also heavy and dense patches of Nitella, sheltering at least five species of rhabdocoels, all active and well-developed specimens. In the deeper portions are large clumps of water lilies and several other flowering plants, such as arrowhead, and floating around at the surface, sheets of Cladophora and other algae. Thus, while the plant life is very profuse, the animal forms are much fewer, and larger types seem lacking. One notes the absence of such ordinary types as frogs, clams, snails, waterbeetles, and dragonflies. Out on the banks a sand toad is common, together with four species of turtles and a little sand lizard. Altogether, the conditions prevailing seem to be ideal for several species of rhabdocoels tho not so favorable for most others.

A rather surprising situation was that encountered in an old boat anchored high and dry in a little clump of willows. It was protected from the wind and open to the sun so that evaporation was rapid. However, the two or three tubfuls of water which the boat contained must have been placed there two months before, at the time of high water, as there had been no rain. The whole boat was nearly filled with three species of Spirogyra all conjugating. It was very luxuriant and harbored copepods, ostracods, diatoms, rotifers, and lower algae. There were no insect larvae, as might be expected, but many species of protozoa and such simple organisms. Rhabdocoels were there in abundance, the ever present Stenostoma and two other species, all thriving in their prison, a little world entirely isolated, but perfect.

Thirty yards away from the old boat was a muddy pond which well illustrates a different type of condition. Early in June, the overflow flood-water spread out over a forty acre corn field; much of it drained away and by the middle of July, only a depth of a few inches was left. For a rod back from the actual water edge the ground was extremely mucky and soft down to a depth

of eighteen inches. Large patches of mud-covered Nitella seemed to be the only surviving species of plant life, growing all along the shore and out to a depth of ten inches. The water was 'thick' and black, with only a few animal forms, except in the case of protozoa which seemed to flourish. Stenostoma was the only rhabdocoel present and all the individuals collected were very long and slender. In this situation absolutely prohibitive for most species, Stenostoma appeared to be almost the only form above the Protozoa which could carry on its existence.

Another type of pond is that used by the United States Bureau of Fisheries. Such ponds are artificial in their origin and are always under control, thus presenting data interesting in comparison with natural conditions. These ponds are either cement lined or have an earth bottom. They vary in depth and shape. Some are shallow, mere tanks with a smooth bottom, while others are long and narrow with a graded bottom giving half a dozen different depths. Often a number of half-partitions supply lurking places dark and secluded. The unlined ponds are generally open and broad with a depth varying evenly up to eight feet. The small tanks are about three by eight feet, while the largest ponds will cover an acre of ground. The water is supplied from a common reservoir, filled from the river. There is always an intake and outlet thru which is kept up a constant and steady flow. The loss by evaporation is thus supplied, the oxygen content kept nearly standard, and the water constantly free from organic debris. The life conditions are much less complex than is naturally the case, since either fish or clams are the only large species present. The vast number of microscopic forms have found their way accidentally and flourish because the situation is favorable. All of the ponds contain a larger or smaller amount of filamentous algae, water weed, and lower forms of plant life. This helps to furnish a never-ending supply of oxygen and a hiding place for huge communities of entomostracans and the like. There is no possibility of a sudden change in the several life factors, i.e., the conditions are constant and steady, a situation which is ideal for all sorts of types and makes the number of species very large. Even during the winter, down under the ice in the deepest parts, the stream of warm intake makes possible a continuance of almost summer conditions, and consequently there is not the wholesale extermination of the species that generally follows the fall drop in temperature. Thus generation follows generation without a break, right through the coldest months.

Many other ponds, permanent and seeming to present conditions suitable for large annual communities, are more or less poor in such forms, and may also be said to be dead water and many which contain various other species do not show planarians or rhabdocoels. Perhaps the most influential factor in this poverty of the fauna is the constant agitation of the water, which, when coupled with a variation in the amount, is sufficient to prevent much life. Then, too, many species are so retiring in their habits and spend so much of

their lives hidden away that they escape notice even tho they are often present. Such is probably the case with many of the creeping rhabdocoels.

Reactions of Worms

This study of biologic conditions is at the outset superficial, and only the most general conclusions can be ventured. Definite and positive statements are to be questioned since so vast a number of factors is concerned, and it is now an impossibility to know or control nearly all of them. Consequently, many observations are qualified and results are guardedly and hesitatingly set forth. But in studying any pond or stream, there are always many details of life habit which present themselves conspicuously, and many of the influences which bring about certain effects can be very clearly recognized.

Perhaps one of the most noticeable reactions is that to the amount of oxygen. For altho supplied with no tissue or organ by which to make direct use of oxygen or by which to effect an exchange of carbon dioxide, the Turbellaria are all quite sensitive to the presence or absence of either. The processes of respiration are carried on thru the skin, the parenchyma, and even thru the general cells of the body itself which are in direct communication with the surrounding water. Thus, altho the amount of oxygen necessary is infinitesimal, there is no reserve store, so that there must be a very constant source. In aquaria, when there begins to be only a slight overloading with carbon dioxide, many individuals can be seen making their way to the top where there is a layer of fresh water. Oftentimes this seems to be the only method of dragging certain species out from their hiding places. They are likely to remain near the top for days, staying quietly near the edge or gliding about very slowly just beneath the surface. Sometimes around the edge of the dish or the tank they crowd up into the little film of water held by capillarity above the general surface. In balanced aquaria, on the other hand, large numbers are often hard to find, since even the deeper portions will be perfectly fresh. If, then, for any reason the balance is suddenly lost, up to the top come several species. Some forms are habitually free swimming and are much of the time to be found creeping over the surface or exploring thoroly the deeper regions. When oxygen is lacking they remain constantly in the uppermost water, avoiding the foul depths. Under normal conditions many species find their most suitable habitat entangled in a mass of alga or creeping over bits of weed, probably as much for the supply of oxygen and consequent purer water as for a hiding place. This last conclusion is evident since in those pools where there is little plant life, all the specimens present are found in close proximity to whatever bits of green algae can be found in the same way that any animal clings to its last source of oxygen.

Planarians which live in locations vastly different from the above seem just as sensitive, for even tho their habitat is running water, not all parts of a stream are equally favorable. For example, the pebbles and rocks in sheltered, quiet pools show no specimens even when the food is ample. If,

however, at any point a little current passes thru, thus raising the oxygen content, at least a few individuals are there. Out in the middle of the river, on the contrary, where the flow is exceedingly swift, making a boiling, seething torrent as it tumbles over stones, the oxygen content is greater. Here the number of individuals in a given area is limited only by 'standing room,' even clam shells and bits of wood being entirely covered. Thus it seems that in respect to their use of oxygen the turbellarians are not essentially different from other higher phyla.

All the turbellarians are, to some extent at least, sensitive to light, but they react toward it in very different ways, so that no general statement can be given. The presence or absence of eyes cannot be taken as the main factor in this response, for altho the eyes are primarily light detecting organs, species in which they do not occur may possess the ability to distinguish between light and darkness. The planarians and rhabdocoels live under such different conditions that a difference in reaction is to be expected.

The planaria are definitely and conspicuously negative in their response both to diffuse and localized light. In three species, common to this region, the eyes are large and well-developed. The animals ordinarily live under stones or in the depths of algal masses where a good deal of precision in their reaction is necessary. If placed in a large open dish, they investigate very thoroly every part and invariably come to rest at the point of greatest shadow. Their ability to estimate the size and density of the shadow is evidently keen, since they seem able to distinguish even small gradations. Another factor which is perhaps to be correlated with the perfection of eyes is the relative amount of color. The pigment which here varies in amount with light and dark locations, is not present, at least to any extent, in forms which do not possess eyes, and it is not an unreasonable conclusion that color and eyes have evolved together.

The rhabdocoels have a more variable habitat than the planaria and are not capable of so exact a response to light, even tho some species possess as highly developed eyes. The color has no direct connection, as for instance, Strongylostoma, a form which has relatively very large eyes possesses no pigment. This is also the condition in several Dalyellias. The members of these two genera are positively heliotropic, except when the light is intensely localized. The genus Stenostoma, on the other hand, is without eyes or pigment and gives a negative response to light, be it strong or weak. These forms do not habitually frequent deep, shaded places but rather a dimly lighted situation. This fact perhaps explains the rather general reaction, and their habit of being content with merely the less lighted regions. This habit, however, is constant, tho in just what way the light is sensed is not known. As a whole, the genus Stenostoma is very simple in structure, all of the reactions being general rather than precise, and this response to light is the most definite of all.

The effect of temperature is very hard to ascertain, in any detailed or definite way, since it is of general influence, having to do with large quantities of water rather than with any very limited portion. In the broad sense temperature

is the main inciting force which every season starts or retards the life processes, and almost never in nature is it found as a localized stimulus. During the winter the ice confines the cold to a layer at the surface and to some extent limits and restricts the extent of its influence. It acts somewhat as a blanket, preventing the cold of the air from penetrating too deeply, so that beneath it a vast deal of life continues thruout the year. It seems certain that rhabdocoels remain in the layer of free water, which is, in fact, their regular habitat, rather than hibernating in the more protected bottom mud. Thruout the winter of 1916 collections were made from a single pond every week. During January and February the Cladophora was dragged up thru a hole in the ice. Two or three species appeared in every haul, altho sometimes not in great numbers. It is, of course, evident that myriads of individuals are killed by the cold every winter, especially since by far the most live in the region of the surface and are frozen. Those which are driven to deeper water carry on their existence, perhaps with not so much vigor, but nevertheless very successfully. Another factor which must be taken into consideration in drawing conclusions is that, with the onset of cold, the manufacture of oxygen is largely cut off and a considerable proportion of the destruction which occurs, results from the absence of oxygen and the presence of an increasing amount of carbon dioxide. As an interesting side light on this question I may note that in artificial ponds where thru the bottom there is a constant stream of pure water all winter long, life continues with unabated vigor. This is, of course, due partly to the supply of oxygen, but the higher temperature also has much influence.

With the melting of the ice in the spring relative conditions in the water are entirely changed. The ponds lie open to the warming influence of the sun and the response in many species is very ready. Thus it is that most planaria and many rhabdocoels become sexually mature at this season. To a great extent it is merely the change in temperature which incites greater cellular activity. Those forms which do not have their reproductive seasons at this time almost invariably go thru a period of very active budding or fragmentation which does not occur when the temperature is very low. Instances which well illustrate the power of heat are to be found in cases where a warm spring flows into a cold pond or stream. There, crowded into the water where the temperature is high, are myriads of animal forms. Among these planaria of all sizes are often very plentiful, while a few feet away, beyond the reach of warmth, there are no specimens at all.

The lowering of the temperature in the fall has two definite effects. First, it retards the life processes of many species and, second, in a directly opposite way, it induces an acceleration in the growth of the sexual elements. The first instance is the more common and has been referred to above. The second is rather difficult to understand. There are perhaps two theories to be offered in explanation. One is that those rhabdocoels which, in their primitive habitat, lived in cold regions become sexually mature when the temperature comes the nearest to their ancestral condition. The other, is that eggs which are able to

develop slowly or lie dormant for some time, if deposited in the fall, will be ready to begin a more rapid growth in the spring.

In the matter of food, the turbellarian is not fastidious. Many pieces of animal and plant material find their way bit by bit into the tiny and apparently inefficient mouth of the hunters. Plant food seems to be second in choice, probably because the thick cellulose of its epidermis is too armor-like and is beyond the possibility of even receiving an impression from the delicate and jawless lips of these gentle feeders. Even the finest of the filamentous algae are themselves as large as many of the rhabdocoels and too stiff to be managed, while the lower forms, such as the flagellate swarm-spores and the like, are as a general rule too swift and active to be caught alive. Even the planarians seem to prefer a more easily assimilated food. When, however, algal cell walls are broken down, so that the inclosed cytoplasmic content becomes available, either free in the water or adhering to its original position, then it is greedily sucked up by almost any species. As soon as any of the lower plant forms begin to disintegrate, then they become a probable food supply.

The obtaining of animal food is also difficult, since only the soft parts can be used. The entomostracans, rotifers, and similar types, furnish large amounts of food as soon as the individual dies, but they are seldom attacked when alive. In one instance, only, has a rhabdocoel been seen making an attempt on the life of a rotifer. For five minutes they struggled, but the rotifer held its ground and the rhabdocoel finally left. The chitinous shield of small crustaceans armed with spines or other projections is formidable, but as soon as the segments of the body thru disintegration begin to fall apart, then it is possible for the rhabdocoel to crawl inside and, thus protected, clean out the soft parts at its leisure. Protozoa probably make ideal food because their protoplasm is generally not so thoroly covered as to be inaccessible and because they are common everywhere. In those species where a calcareous shell is secreted, the rhabdocoel swallows the whole, digests out the protoplasm, and then ejects the hard parts. Tho the planaria are often dependent for their food on disintegrated fine organic debris, yet when the opportunity offers they make the most vigorous efforts to obtain the flesh of higher animal forms.

As a whole, the turbellaria are scavengers, living upon bits of disintegrating organic matter. In the general life constituency of a pond community, they play an important part, constantly searching out and devouring particles which might later be a source of bacterial growth. The smaller rhabdocoels can be found in great numbers, incessantly hunting thru the mazes of algae for dead crustaceans, etc., or burrowing and worming their way thru the loose earth-like masses on the surface of the bottom. Here they find what is left of myriads of protozoa and also other material, either plant or animal, which they speedily devour.

Animals with feeding habits such as these would seem always to have more than a sufficiency of food supply at hand. This is not always the case, however. Under special conditions, other worms or larger species may keep the

sources of disintegrating matter completely used up, or masses of debris may be washed away to such an extent that a whole area is entirely cleaned of its food content. Under such conditions the turbellarian does not die immediately. It goes thru a process of starvation so slow as to be almost unnoticeable. The individuals become thinner and smaller and shrink gradually until in some specimens they are no more than one-fifteenth their original size, at the same time becoming almost transparent in color. This explains the immense amount of variation in size of adult forms, the individual dimensions depending directly upon the food taken.

The enemies of the turbellarians are few. Altho such delicate animals are evidently almost entirely defenseless, they manage to carry on a fairly free and unhampered existence. The smaller species spend much of their time swimming slowly in open water where they encounter almost all the other inhabitants. It is especially noticeable in aquaria where many species collect at the surface or towards the light that the rhabdocoels or planarians mingle constantly with the others, crawling over them and around them in the most unconcerned manner. And often two or three individuals will collide with each other without the slightest inconvenience or apparent fear. This is easily explained in the case of the planarians which are enormous compared with the tiny crustaceans, but the rhabdocoels are so nearly the size of the other common types that they seem possible prey. However, a number of times rhabdocoels have been found gliding unharmed directly thru between the valves of an ostracod or resting contentedly under the edge of the carapace of a cladoceron.

This situation may be due in part to the fact that the crustaceans themselves habitually live upon disintegrating material and are not likely to attack living forms. Then, too, some of the rhabdocoel species possess nematocysts which would make them not only unfit for food but also rather well protected from most enemies. Others which do not possess stinging cells have especially developed dermal rhabdites in very great numbers. While these are not weapons of defense, they probably render the individuals unpalatable.

Perhaps the most effective method of protection is the general habit of retiring to well-guarded situations. A flat worm lying close on the underside of some rough stone is in a fairly safe place, where few hostile species are capable of dislodging it. The rhabdocoel hunts in some mass of alga where, at the same time, it is completely hidden from many large forms. If, however, it encounters an enemy of any sort, the rapidity with which it can contract enables it to disappear.

MORPHOLOGY

FAMILY PLANARIIDAE

In number of species the Planariidae are more fully represented in the inland states than any other family of the Turbellaria. Seven species have been identified, five of which are new. *Planaria maculata* Leidy (1848) is the most common of these, occurring in abundance in nearly all rocky streams and in many quiet ponds. Others appear more rarely but over such widely separated areas as to suggest that they exist in much greater frequency, and in larger numbers than is generally supposed. One of the species with such a widespread habitat is that mentioned next.

Planaria velata Stringer 1909

This worm has been taken from two very different localities, one a temporary puddle at Urbana, Illinois, the other a spring at Homer, Minnesota. At the former place the water was black and muddy with only a minimum amount of algal growth; the specimens came from the bottom mud, with the loose silt, leaves, and sticks dragged up in a dip net. The conditions in the other instance were almost the opposite. The planaria came from a warm water spring flowing into the Mississippi and forming a little cove where almost summer conditions prevailed even during the coldest weather. All the collections both at Homer and at Urbana were made in February and March. Then a large number of species flourished. The plant forms and protozoa were especially luxuriant so that an ample supply of food was furnished for a well populated community of microscopic forms. The list contained several rhabdocoels which were present in great abundance, and at least two planarians. One of these, *Planaria velata*, was conspicuous among the other forms by its dark brown color and lines of fragmentation to be explained later. There was some characteristic variation but most of the specimens were dark. Those few which did show a light gray were the small regenerating individuals. The color is due, as Miss Stringer says, to a yellowish-brown pigment which causes the general dark tinge, but which under a lens is surprisingly pale and clear against the almost transparent groundwork. This pigment is arranged in very small spots, either round or irregular in shape, and lying in rows. These rows are parallel, placed very evenly, close together and are waving instead of straight. In general, they run longitudinally, but every projection of any part, every indentation, every wound, causes a fusion or else a break of the rows around it. Moreover, thruout the mid-dorsal region both rows and spots are smaller and denser, which explains the heavier color of the upper side. The pigment spots within the rows vary in their relation to each other. They may be large and close together or far apart; they may be evenly separated or not; or they may be small, scattered, or collected in

groups. Under all conditions, however, there is a fine line of connection from one spot to the next. This is sometimes hardly more than a suggestion of pigment, yet in some places the connecting thread is beaded and heavy. These color masses are all situated in the deeper portions of the epithelial cells.

The smooth color was often interrupted by light gray lines running in different directions across the body. In some specimens these could be seen as grooves or furrows running into more or less conspicuous notches at the edge of the body. It is along these lines that later the splitting into fragments occurs. Often more than one or two lines could be distinguished at once and very probably in some specimens there might have been several, since Miss Stringer reports as many as thirteen fragments from a single individual.

That the lines of fission appear so early in the pigment and skin is noteworthy, since in some species the internal divisions are laid down before the external are very prominent.

Planaria maculata Leidy 1847

Figures 43 and 44

In the collections which have been made in the past, *Planaria maculata* has appeared often and in large quantities. The situations in which it lives are necessarily varied, and often they are entirely opposite in many respects to those where it has been found previously. Then, too, the immediate make-up of a pond or stream generally changes somewhat within the length of each season, and much of this change is detrimental. Another point to be considered is the lack of protective details, for, from many of its enemies it has no escape. A summary of these conditions will explain the very apparent differences in structure among the individuals of even a single pond. The variations are mainly those of size, shape, and color, and since a very large percentage have suffered mutilation, there are always many specimens which show parts in some stage of regeneration. Thus, structures may be altered within wide limits and the animal still be fairly typical. For these reasons, when many planarians from the Rock river showed small eyes, the fact was hardly noticed, and it was not until large numbers revealed the same character that special attention was given to it. Several hundred specimens were taken from different places along the river, all with this same distinguishing mark. Other collections in the Mississippi river, at Homer, Minnesota, at Fairport, Iowa, and also in the adjoining ponds, manifested the same feature. In most respects, the characters are clearly those of *Planaria maculata*. The variations are of the same general nature, the habitat the same; the conspicuous differences are only in the size of the eyes and in the surrounding pigment. Exact measurements were taken of the eyes in a few specimens from every collection and approximate comparisons made for several thousand more. There were always to be found a number of individuals with clear white optic regions, lacking entirely any eye pigment, and there were always individuals with eyes at some stage of regeneration.

These were carefully excluded from the general results. The dark pigmented portion was measured for both length and width with some note as to the shape. From several hundred specimens measured, the average varies between 113μ and 167μ in length and 8μ and 31μ in width. In general, the eyes are a fairly regular kidney-shape but the percentage of difference between the two eyes of the individual is high. This, however, is true for all planarians. These measurements were very nearly one-half those of an average *Planaria maculata*. The pigmented mass is a little more solid, not inclined to be a crescent and always broad in proportion to the length. The position of the eye is also significant. In the river type, the eyes are always very much nearer the median line than in the pond form. Thus they lie almost in the edge of the middle pigmented stripe of epithelium. This situation makes their relation to the whole of the unpigmented region somewhat different from that of the common type. That is, lateral to the eye-pigment, one finds a very large irregular clear area. This is about five or six times the width of the eye itself, and is striking in its transparency. In the pond type, on the other hand, the clear region, altho varying to some degree and irregular in outline, fits closely to the eye-pigment leaving only a wide margin of transparent integument.

This special character seems to be constant for the individuals found in the Mississippi river or its immediate vicinity. Whether it is only an environmental change due to some immediate biologic condition or whether it is developmental, remains to be seen.

Planaria truncata Leidy 1851

About the first of November, one specimen which was clearly *Planaria truncata*, was found under a stone in a little rivulet at Milwaukee, Wisconsin. The stream was hardly more than a trickle bubbling down a narrow wooded ravine. About fifty yards back from the shore of Lake Michigan, just before reaching the sand of the beach region, the water splashed over a number of large stones. Here was a large fauna of crustacean and protozoan species with a few bits of algae in the quiet pools. Among other things on the protected side of a well-washed pebble was the large white planarian.

It measured about 14mm. in length and was plump and well fed. The species characters were very noticeable. The sharply truncate head with small dark eyes set near together and far posterior, the rather long conspicuous pharynx, the white or translucent appearance and the much lobed digestive tract, were all details which made the identification evident. Of these points, the significant structure of the intestine is perhaps the most remarkable. The contained food material was a light brown which contrasted well with the surrounding white tissue. The intestinal wall, since it was very definite and to some extent non-elastic, made a clear cut outline to the digestive tract, so that the fine fingerlike branches stood out by themselves. The fact that these branches do not anastomose but retain their individual shape and constant

position, was visible to the naked eye. Thus the intestinal anatomy is conspicuous in a way unknown among other planaria. The structure as a whole is especially well defined and all the parts easily distinguishable.

Family Catenulidae

The family Catenulidae was created by von Graff in 1905 to contain five genera, two of which, Stenostoma O. Schm. and Alaurina W. Busch, had, up to that time, been grouped under the family name Stenostomidea, and a third, Microstoma O. Schm. had belonged to the Microstomida. To these three, he added two others, Rhynchoscolex Leidy and the old Catenula Anton Dugès, which had hitherto been grouped by itself, seemingly unrelated. He took the name of the new family from the oldest genus. Two years later, in 1907, Alex. Luther added the genus Lophorhynchus, a species with very heavy pre-oral furrow. Then, on the basis of the paired excretory tubules, and in agreement with the researches of Vejdovsky (1882), Sekera (1883) and himself, he removed Microstoma and Alauria, putting them together to form the Microstominae, a sub-family of the Macrostomidae. Another change came in 1908, when von Graff substituted the generic name Fuhrmannia for Lophorhynchus, since the latter was already in use. The list of genera belonging to the Catenulidae was thus 1) Catenula, 2) Fuhrmannia, 3) Stenostoma, 4) Rhynchoscolex, and this classification now stands.

This family is the simplest of the rhabdocoel group. It is characterized by the lack of an anterior prolongation of the intestinal cavity, and by the possession of a single protonephridium. The testes and ovary are always unpaired, tho in general they are not to be found since periods of sexual maturity are rare. The common method of reproduction is by budding and chains of two, four, or six zooids are much more frequent than single individuals. Without eyes or rhabdites, almost entirely lacking in color, these forms are most inconspicuous. With good reason, have they been likened to large protozoans, and superficially, at least, seem to be entirely without specialized structure; they are always small, few in number, and compared with other types easily overlooked.

Of the four genera, three have been reported from this country. Many years ago one species of Catenula and two of Rhynchoscolex were collected in small numbers around Philadelphia. They are probably present in other places in the eastern states, but have not yet been found west. The genus Stenostoma is quite different in its distribution. Several species have been described from very separated localities and the genus as a whole seems to have a rather wide-spread occurrence. It was first described by O. Schmidt (1888), who recognized the characters which separate it from Microstoma. He named two species and during the next thirty years eight others were added by different investigators. Up to 1905 the genus name was Stenostoma, then it was changed to Stenostomum, without adequate reason, I think. In the United States, two European species have been identified, while four new ones

have been added. This is the most important genus of the family, since it is by far the largest both in number of species and number of individuals. Altogether, there are sixteen species, one being a salt-water form. Then, too, the feeding habits make it seem to command an economic importance.

The most noticeable details of structure are the rather large sensory pits on either side of the head. These are unique and extraordinary in themselves and probably take the place of the statocyst, eyes, and sensory organs of other types. The blunt, somewhat stiff anterior end and the protruding mouth region give a special shape and appearance to the head. The comparatively large intestinal cavity, filling so nearly the integumental sac is an other conspicuous character. Altogether, these forms are worthy of more than ordinary interest.

Stenostoma leucops (Ant. Dugès) 1828

Figures 50 and 51

Of the sixteen species which make up the genus, the oldest, *Stenostoma leucops* (A. Dugès) 1828 has had the most attention. The original description was full and exact. Almost nothing more was done with it until H. N. Ott in 1892 made a careful and complete study of the histology of all the body systems, bringing out a number of details of value for comparative work with other families. Since this form is most primitive and evidently nearest the ancestral type, all characters of structure are of especial interest. In an experimental way, several authors have made extensive researches. C. M. Child during 1901-2 and 1903 published a series of five papers dealing with the development of the zooids and regulation of fission using both this species and *Stenostoma grande*. His results explain, at least to some degree, some of the life-habits and variations always to be noticed. Since the asexual reproduction is the general method, individuals in all stages of regeneration and development are to be found together. One or two of his general conclusions throw light on the laws which govern these common processes. Perhaps the most important are the following: When a zooid separates from the chain thru injury, "complete destruction of younger parts by older, may occur, but not older parts by younger." Again, "if the separation from the parent is very early, the anterior portion of the younger individual develops a brain regardless of its former relationships." These two facts will account for many of the half changed shapes and conditions present in smaller specimens. Ritter and Congdon (1900) have also used this convenient form as the basis of a series of experiments having to do with fission induced artificially or inhibited in some manner. These authors emphasized the migration of the brain ganglion and also certain special laws of regeneration which seem to hold. Child does not agree with these findings and brings forth rather exhaustive data to prove the truth of his own conclusions.

The use to which this species has been put is due partly to the simplicity of structure, and consequent simplicity of reaction, partly to convenient

size, and partly to the abundant supply of individuals. The distribution is very much wider than was earlier supposed. Silliman (1885) was the first to find it in the United States. He discovered it in large numbers in certain ponds in the east. The knowledge of its occurrence in other places came slowly. Every few years it was reported from some new locality, but not until within the last fifteen years have the collections been adequate enough to prove its presence common thruout the country. Now it is known to be living in three-fourths of all the ponds wherever there is other animal or plant life. During the winter under the ice it seems to carry on a successful existence and can generally be found at any time. Of the whole group of rhabdocoels this species is the most common, in fact almost cosmopolitan, and it is likely that future collections will prove it entirely so.

In the way of biologic relationships, some few new observations may be of value. One character which makes possible the very general habitat is the ability to exist under varying conditions. *Stenostoma leucops* is able to live in situations where the oxygen content is extremely low and where often the amount of carbon dioxide present is so large as to kill other members of this group. This explains the fact that it may be present in small puddles and ponds where there is almost no plant life, or in places where few animal types exist. Often, too, in cases where the water is thick with bacterial growth and disintegrating material of all sorts, this Stenostoma is able to live long after the conditions seem entirely unfit. That it is sensitive to the presence or absence of oxygen and carbon dioxide is shown when specimens are placed in water where part of it is clear and fresher than the rest. They invariably find the freshest parts, even tho the difference be very slight, and are always to be found in the clearer portions of an aquarium.

The reaction to light is negative, tho not very prompt or definite. That is, the specimens are always on the side of the aquarium away from the light but it takes some time for them to find that position and many seem not to prefer the very darkest places. It may perhaps be said that both the brightest and darkest portions are unfavorable, and that subdued light is preferred.

The reactions are not at all precise or prompt and the animals seem to be sensitive to general influences rather than to direct stimuli. Heat and cold in a general way seem to have almost no appreciable effect. Small weak individuals are found as well in summer as in winter; large plump specimens in cold as well as in warm water, and, too, the period of sexual maturity is not so exactly dependent upon change in season and consequent change in temperature as in most rhabdocoels. It is true that in winter, in ponds where a small stream of water raises the temperature, the numbers which find the warmer parts are very large, but other conditions very probably hold here, since in such places there will be more food and often since the water is fresher, more oxygen. As a whole, the response to any ordinary stimulus is never strong. If the stimulus is so intense as to cause a decided reaction, it is then of such a nature as to be injurious or perhaps fatal.

The food relationships are more complex than appears at first. How many enemies there may be is hard to ascertain. That Stenostoma becomes the food of other species is not easily determined since the body is entirely of soft parts and quickly disintegrated. They seem not to be hunted down by other forms to any great extent, except in the case of some few fishes which easily take them along with other microscopic species. When, however, the body structure is disintegrating, the protoplasmic content within the rhabdite-bearing integument is good food for almost any form. They can hardly be said to form any conspicuous part of the food of an animal. The food they eat is of much more interest and importance. To some extent they are scavengers, eating the disintegrating organic material so plentiful in the surface of the bottom-mud, or entangled in masses of filamentous algae. They are voracious hunters and can nearly always be found working their way, truly worm-like, thru the soft silt, systematically seeking out every bit of available nutrient material. They also evidently swallow much indigestible matter, as after a period of feeding in such a situation, the intestine will be found almost black and later this residue will be seen extruded thru the mouth, sometimes a little at a time, and often in quite large masses. That this common form plays a large part in helping to keep clear the bottom water is very evident. The small algal swarm spores, volvox, euglena, and the like, are eaten to some extent, but are probably more or less unpalatable. The food which is the most conspicuous, altho hardly the most common, is made up of the larger animal types, such as ostracoda, glochidia, encrusted protozoa, and the like. *Stenostoma leucops* especially seems to have a liking for the largest possible morsels, preferring those with a hard shell. Difflugia is, perhaps, the most common form found lodged in the intestine and is present in even rather small-sized individuals. During a few days, five different species of Difflugia have been seen within the digestive cavity of specimens from a single pond. The naked protoplasm of the animal part, even tho entirely drawn into its shell, is easily digested out and the comparatively smooth spherical exterior makes a mass easily extruded. The size is also convenient, not so large but that even the contracted zone of fission may allow it to pass thru to the posterior zooids. In the same way, other small smooth forms seem especially desired. One example will show the tendency in this direction. An individual was noticed swimming around normally except that the movement was a little slow. The shape, however, was conspicuous as the animal seemed to be a tiny cross, very clear-cut and definite. Under the the microscope, the extra structure proved to be a good-sized ostracod lying in the intestinal cavity of the worm at right-angles to the length of the body, and by its bulk causing the body-wall to be pushed out on both sides until the protruded part was equal to the other divisions. The animal seemed to suffer no serious inconvenience altho the integument and intestinal wall were stretched to the breaking point. Evidences of such inappropriate food are quite common. Any rounded hard-shelled animal seems acceptable either

in part or entire, and the Stenostoma will often attempt particles entirely too large to be managed. Spiny, rough, or even slightly irregular bits are almost never touched altho they may be small and easily captured. That very large bodies can be passed thru the slender pharynx is evident, if the more or less constant dilation and contraction be noticed. When the intestinal valve is closed and the long pharynx is collapsed, it appears as only a narrow line running back from the buccal indentation. At various intervals, often rather suddenly, the mouth is opened, very wide, so that its diameter is nearly that of the body, then immediately the pharynx is dilated almost to a sphere, displacing the parenchyma of the surrounding region and giving almost a globular shape to the head. It is this elasticity of the walls and enveloping parenchyma as well as the heavy muscular contraction which give the possibility of extended variation both in size and shape. The intestinal opening is also capable of enormous distention. The extreme flexibility and lack of cell intimacy have been mentioned as one of the important characters of the phylum and the development of such a character seems to have reached its height in this species, a fact which to some extent explains the variation in the size of the food taken.

Another striking detail of appearance is the difference in shape, size, and number of zooids among individuals not only of several ponds but those from one part of a single pond. This difference in appearance is the result of the formation of zooid chains, and all stages of growth are to be found present at almost any given time. In localities where conditions of food, oxygen, and temperature are ideal or nearly so, the chains of zooids form rapidly, and the segments cut off are small and blunt at first, altho they elongate very soon. Child (1902) worked out very thoroly the history of regeneration and the stages thru which the segments pass before they are themselves ready to divide. It is commonly known that almost immediately upon being separated, the segments invariably attach themselves to some convenient substratum. The subsequent shape, Child says, is the result of this habit, and the "elongation of the body can be prevented by preventing the animals from attaching themselves." His final conclusion is of especial interest. "Due to attachment of animals by the tail, and to mechanical tension caused by ciliary action, the form of vegetating pieces is changed; it is a mechanical phenomenon and not the effect of stimuli." The truncated, anterior zooid after the cutting off of the others, is a conspicuous shape very frequently seen. It can never attach itself and so rather aimlessly swims about stiff and awkward until the rounded short posterior end begins to become normal. In no other type is the shape so entirely dependent upon physiological condition or relative age. The number of zooids for this species is generally two, altho longer chains are often to be seen. This is due to the fact that fission planes are rarely interpolated between others and that the first division takes place before a second zone of division begins. This is quite the opposite condition from that in Microstoma, where, when fission planes are laid down at all, they very closely follow each other. It may be said that in Stenostoma the asexual budding is not to be correlated

with any season or with environmental conditions, since it is a constant process, but that the rapidity of the growth of zooids, i.e., the number of generations developed, is dependent upon these surroundings.

Stenostoma tenuicauda von Graff 1911

Most often in ponds where *Stenostoma leucops* is present, in larger or smaller numbers, there may be also several different species of rhabdocoels, but generally no other members of this genus are to be found. In several of the ponds at Fairport, Iowa, however, *Stenostoma tenuicauda* was also present and was in this instance the more frequent with very nearly the same life-habits and the same environment. The two species existed side by side, but there was a great difference in their rapidity of movement. *Stenostoma leucops* is much more regular and quiet, holds more constantly to its course, while *Stenostoma tenuicauda* shows a tendency toward a greater amount of action. In appearance, too, they differ decidedly; while the former is slightly opaque, the latter is quite clear and transparent, slightly yellowish in tinge. The slender tail region is also conspicuous when taken together with the blunt and heavier condition in *Stenostoma leucops*.

Stenostoma giganteum nov. spec.

Figures 46 and 48

This species was collected in numbers in a clear pond with sandy bottom near Grandview, Ia. The water was very warm at the surface and cold a few inches down. The drainage area was small, with no direct inlet, so that under all ordinary conditions very little outside water entered and since most of the water was seepage, there was no chance for any number of species to be washed in. A small rivulet carried off some surplus, but for the most part all current was lacking and in fact not even a disturbance of wind could be detected. The conditions were very nearly those of a balanced aquarium. The comparative shallowness, with sandy surrounding area prevented any silt from being deposited. Then, too, the amount of disintegrating organic matter was minimum. The plant life was profuse, enough to take care of all the carbon dioxide generated, so that the water was always clear and fresh. The animal life was composed of a few fish, mostly Amia, a few stray turtles, microscopic forms like small crustacea, protozoa, and many rhabdocoels. The lack of disturbance or change and the constancy of inter-relationships of various species precluded the possibility of great differences in the general fauna and flora and brought about persistence of the same types and a continuation of the same relative conditions. The situation in the present instance was, perhaps, slightly different from that of other years, since by a break in the shore line the river had swept down thru the pond carrying away the whole thing. As a result all the pond life was new, at least only that left when the water receded. The rhabdocoels were floated out from masses of Chara pulled up from the bottom where the water was eighteen inches deep, but they were

not to be found in any of the masses of Spirogyra taken only a few feet away. The coarser leaves of the Chara evidently harbored more protozoa, and more organic debris thus furnishing a larger supply of food, but the oxygen in that region must have been very much less. No specimens were taken at the surface. They were always down a few inches where the water was quite cool. *Stenostoma leucops* was present in only small numbers and *Stenostoma giganteum* was very numerous. The food seemed to be almost entirely protozoa and small crustacea, the size of the worm making it possible for it to swallow easily individuals of different species.

The movements were invariably slow and the twistings and turnings so characteristic of *Stenostoma leucops* were very nearly lacking. Most of the specimens were made up of two zooids, and not a single chain of more than that was found. They were negatively heliotropic. Their length of life has not been ascertained, as they were found only during the summer months. A number of collections were made during January, under eighteen inches of ice but the very shallow water below this thickness showed only a very few crustacea. Dead fish were seen and it was apparent that very little oxygen was left in this bottom layer.

The relations with other forms seemed quite simple. The only enemy of this Stenostoma was probably the fish, and the whole life condition was without great struggle.

Among the other animal types to be seen in the collections, this species was very conspicuous, even to the naked eye. It was the largest of the nearly microscopic forms and moved quite enough to be easily distinguished. As has been mentioned, ninety percent of the specimens were composed of two zooids, and such individuals averaged in length from one to two millimeters. The two parts were not quite equal, the anterior generally being a little the longer, so that measurements would average about 0.7 to 0.9 mm. for the posterior segment and 0.8 to 1 mm. for the anterior segment. The single individuals were, as a rule, those which had lately split and were of ordinary condition. They were almost always a little over one millimeter, but never reached the length of 2 mm. The width and depth were very nearly the same except in the tail region and in the very anterior end. This diameter was from one-fifth to one-quarter the entire length of a double individual or in many instances where a separate segment was measured, was as much as one-third the length. On the whole, this species seemed about twice as large as the common *Stenostoma leucops*.

In shape, these specimens are quite different from other members of the genus. They are not so slender, but seemed more stubby and rod-like. The ratio of diameter to length is 1 to 4 or 5, rather than 1 to 7 or 10. Not so agile or flexible, they seem stiff cylinders, tapering off bluntly to a short tip. That is, from about the middle of the posterior zooid to a point just behind the mouth, the diameter is always the same (except at the fission plane). The region around the mouth is somewhat protruded as a sort of circular lip which

on the posterior ventral portion is somewhat extended, making a bulge or knob-like enlargement at that point. The dorsal anterior part is only slightly inflated and slopes up to the anterior proboscis or lappet-like front end. This is a triangular flat portion extending back behind the ciliated pits. The greatest width of this triangle is nearly equal to that of the body in general but the thickness is not more than one-half the body depth, so that the mouth enlargement is accentuated. The shape of Turbellaria generally depends on the amount of contraction or expansion but here the rather unwieldy body is never much altered. That is, the animal is flexible and capable of contracting within very narrow limits. The most contractile portion is, of course, just behind the mouth region where the extreme flexibility of the pharynx demands heavy muscular action, and the muscles of this part are much more thoroly developed than those of any other species. Such a condition can be correlated with the heavier kind of food. The regions of greatest contraction show clearly in the preserved material, where the anterior tip and pharyngeal regions are drawn back into the body integument.

The color appears white. Since the body is heavier and thicker than most forms, it is opaque and not at all transparent. The heavier integument and thicker layer of parenchyma obscure the intestinal contents and also the intestine itself, so that there is no chance for any color to shine thru. Against the dark background of water, these individuals stand out strikingly.

The integument is, of course, a one-celled layer, a little heavier in proportion than that of other species. It is not so transparent as might be expected, due to the rather solid outside walls of the cells, but in most respects is not very different from the general type. The thickness varies with contraction. In life, it is about 10μ, in mounted sections it is close to 17μ over all the body except the anterior and posterior ends, where it is from 20μ to 25μ. That the cohesion of the cells is slight is evident in prepared material where many of the cells are practically pushed out or even completely dislodged from their original position in the epithelium. When the whole structure is thus crowded, the cells dove-tail into each other to some extent. They are then high columnar, but more or less irregular, almost trapezoidal often, so as to fit compactly. The portion containing the nucleus is the larger and with few exceptions is the inner part. The nuclei are large and stain heavily so that they form the most conspicuous part of the integument. In sections, they stand out against the very fine delicate cytoplasm. The cilia are very fine and long, from 16μ to 20μ. They are of about the same size and are distributed evenly over all the body. They move in waves from anterior to posterior as a general rule. The cilia lining the sensory pits and mouth indentation are longer than the others and very even. The ventral side is not so much differentiated as in most species and the cilia are little different from those on the dorsal side. At one point near the posterior end, however, where the animal habitually attaches itself, the epithelial cells are heavier and the cilia show a tendency to be short and large. Another detail not so conspicuous is the presence of very small, clear

rhabdites; where the integument is expanded they lie flat, parallel to the surface but scattered and more or less irregularly placed with regard to each other. Under heavy contraction, when the cells are narrow and deep, the rhabdites are perpendicular to the surface, arranged evenly as a layer on the outermost surface, just beneath the cilia. They are even, smooth little rods with blunt ends and are all of the same size, and occurring over the whole surface of the body. The influence of killing and fixing agents often slightly swells them to transparent knob-like bodies.

The integument is very closely related to the muscular system which lies just beneath it. As Ott (1892) states, the outside layer, next the epithelium, is composed of circular strands while that inside toward the parenchyma is longitudinal. The circular muscle cells are many and make a single row of almost round cells extending the length of the body. This row of cells is interrupted at the fission plane and in the region of the ciliated pits. The several individual strands are often 20μ apart, often side by side. The cytoplasm is granular and stains heavily. The longitudinal cells are very slender strands with the nuclei showing as tiny enlargements along at different points. They are not many in number and are scattered. Very few run directly longitudinal, most being slightly oblique or extending from one portion of the epithelium to the intestine, or to some other part. The layers around the pharynx and mouth have the cells lying much closer together and on the whole they are longer. Around the wall of the intestine, the circular strands and also the longitudinal are almost embedded among the digestive cells. They show somewhat scattered and heavily stained between the outer ends of the light large cells which make up the assimilative layer. When the intestine is filled and the small amount of parenchyma pushed away, these muscle strands are close to those of the body wall. The most striking characteristic of this system is the extremely small number of strands or fibers thruout the whole structure. There is much less true muscular contraction than in almost any other family of this group and a great part of the movement of cells is due to changes in physiological condition.

The parenchyma is extremely vacuolate and the cells are very delicate. Most of the support given the different organs and also the stiffness of the body as a whole, is due to the turgidity of these few parenchyma cells and to the watery protoplasm which fills the vacuoles. As Ott finds for *Stenostoma leucops*, the space between the intestine and body wall contains very few cells and the only material to be displaced under varying conditions is the body fluid. The largest mass of parenchyma is that just posterior to the brain and surrounding the anterior portion of the pharynx. In prepared sections, this shows as a very irregular network with very few nuclei, many of these connecting strands are broken and the cell bodies torn. The body of the cell is rather small but varies somewhat. The nucleus is round, and stains deeply, showing large granules. There are generally five or eight longer or shorter threads or

processes extending in all directions and forming a connection between neighboring parts. The simplicity of this system is one of the characters of the genus and this species seems to have fewer parenchymal cells than any other.

The digestive tract is the most noticeable part of the anatomy. The mouth with its enormous stomodeal indentation is conspicuous. The comparative size of this hollow epithelial-lined portion is suggestive. The mouth proper is situated at the inner end of it and is the point where the true ectoderm ends. It is, of course, flexible and is controlled by a few strands of muscles. In the main, however, it opens or closes as a result of the expansion or contraction of the pharynx. The pharynx, when expanded to its limit, reaches the body wall and even distends it, making the whole of that region appear round. This amount of enlargement is greater than in any of the other common species. In other respects it resembles them, as in the presence of gland cells connected with the outer wall and the lining cilia. The entrance to the intestine is not as sharply marked off as in some species and this opening is not precisely governed as is the mouth. A very few muscle cells surround it but they are not strong enough to act as a sphincter so that the closure is made by the pharynx. The intestinal wall is perhaps the most specialized part of the body structure; altho made up of only one thick layer of cells it shows a surprising amount of variation. When not inflated by a large amount of food, it is thrown up into a series of rather regular folds. The outer portions of the cells under certain physiological conditions show a protoplasm very finely granular, in fact almost clear. It is these portions which undergo most of the pressure and stress when the intestinal shape varies, and they generally are much narrower and smaller than the inner half of the wall. This inner border is often very irregular, some cells being pushed far out into the intestinal cavity. This is caused either by the crowding of the outer margin of the wall or by the internal pressure of the cytoplasm. For, as the assimilation process progresses, the protoplasmic portions of each cell acquire relatively large amounts of food material, generally in the shape of oil globules. Sometimes the contained mass is so large as to occupy the major portion of the cell and gives it a very characteristic appearance. Other cells so situated that only a narrow section of the inner surface is free may have no extra material and be small and shrunken. Thus in most respects the intestine is an organ very like that of other species.

By slightly flattening the animal the simple excretory tubule can be seen contracting slowly and irregularly. It is large enough to be clearly distinguishable and its course can be followed from the posterior part forward to the anterior loop and then back to the external opening. The diameter is about that of the thickness of the integument and the white color makes it stand out against the dorsal wall of the intestine.

The reproductive organs have not been studied since the period of maturity occurs rather seldom. Yet asexual budding is common. All of the specimens taken were either in the process of forming zooid chains or had evidently just separated. The first or median fission plane was the only one developed

completely enough to be noticeable externally, as a consequence almost all the specimens appeared to be formed of only two parts. The reason for this is the precocious or rapid development of the organs in the first budding zone, so that the separation takes place before the organs of the next zone have become visible from the exterior. Sections of such a zooid chain show the relative development of the several parts The situation is briefly this: The brain ganglion on the dorsal side and the buccal indentation on the ventral side of the digestive tract become about half-formed before the integument and parenchyma begin to narrow in at all. By the time this pushing-off process is nearly complete, the mouth has broken thru, the sensory pits are formed, and the last connection is by means of the intestinal cavity which is continuous thru the proboscis-like anterior end of the posterior zooid. In this species, such a connection remains intact for a longer time than in most others and it is broken off only just before the two individuals separate. Generally, in both individuals of such development, a histological examination will show the beginnings of another fission zone in the start of a new pharynx and another brain ganglion. The fission plane here is quite exact and sharply cuts the parts, while in some forms the constriction is gradual so that the adjacent parts do not lie very close together.

Comparing this species with others of the genus, it seems very blunt and solid by the side of the more slender, agile types. The proportion of diameter to length is very much greater than is common.

Since writing the above I have had the opportunity to see this species living in one of the ponds at Fairport. During the early part of July the numbers were so great that a canton flannel cloth was used to strain them out from the water running into some of the smaller tanks. Their presence caused much anxiety because it seemed probable that the food was at least in part made up of glochidia. The individual rhabdocoels were white and opaque, conspicuous and up to 3mm. in length, larger than other specimens of the same species. They exhibited the characteristic stiff cylindrical form and the usual two zooids. One strange fact, not yet explained, was their almost complete disappearance by the first of August.

Stenostoma glandiferum nov. spec.

Figure 47

This form was present in several ponds in which the bottom was muddy and covered with a fine layer of silt. The plant and animal species varied, but in all cases the environmental conditions were much the same. Except in one pond, the sun and wind had much effect upon the temperature and quietness of the water. *Stenostoma leucops* was also present with some degree of frequency. There was always either some filamentous alga or Chara, and the living surroundings were ideal for all types of microscopic animals. Most of the food material seems to be taken from the silt and very little from other

sources; that is, this species is entirely a scavenger in its habits. Altho swimming free when disturbed, and often at other times quietly gliding around, it pays no attention to any food material and only feeds when hunting thru the thick bottom debris. This accounts for the fact that the intestine is always very dark in color. But in general the life-habits are very similar to those of related forms.

In a study of the anatomical details a few characters are significant. The average size is about 1mm., altho, of course, there is the same variation as in other members of the genus. The shape, however, is more characteristic and definite. It is very slender with little difference in diameter. The relative proportion of width and depth to length is about one to eight, which is quite different from some others where it is one to five or six. The anterior tip in front of the mouth is shorter than in most species, a condition which gives the head a much shorter, blunter aspect. The shape of this end is also less pointed than is often found. The posterior portion is short, that is, the diameter of the body remains the same to a point about one-fifth the length of the body from the end. Then the sloping off to the posterior tip is very rapid and this end is nearly as rounded as the anterior end. The body, altho so regular, is not at all rigid and bends easily. The color is light, except in the intestinal region which generally shows up quite dark, making a decided contrast between the anterior quarter where the head and pharyngeal portion is nearly transparent, and the heavy body part.

The integument is very thin, delicate, and transparent, which allows the internal condition to be easily seen. The cilia are short and very evenly distributed thruout, being only slightly longer in the mouth region. The rhabdites correspond closely with those of other forms, being very small, regular rods scattered thruout the epithelium and lying parallel to the surface. Several are often grouped, lying side by side, but many are single. The parenchyma is exceedingly transparent and is concentrated in the head region anterior to the digestive cavity. The posterior triangle between the intestine and the tip is very small and generally almost obliterated. The layer enveloping the intestine is so thin as to be very nearly lacking, its presence being demonstrated only at the fission planes where it forms a mass gradually increasing and pinching off the digestive cavity.

The most noticeable structural character, is the digestive tract. The mouth expands into a somewhat irregular round opening, but does not contract to such a small cavity as in some species. The mouth indentation is a deep funnel rather heavily muscular which is not so flexible as in types having the habit of swallowing large masses of food material at one time. This funnel leads to the pharyngeal cavity which is long and narrow. The wall here is very transparent and the outside cells small and almost invisible. The connection with the intestinal portions is very sharply marked by a deep constriction. Except when the opening is partially expanded, the pharynx appears pinched off completely. The lumen of the digestive cavity is small and fairly

regular in general outline. The wall, of course, is folded more or less but the folds are nearly the same size and follow one after the other about the same distance apart. Within this wall, or rather very closely applied to the outer surface, are numerous masses of cells. These are a little longer than wide and are scattered regularly over the whole intestine. Von Graff (1911) figures intestinal glands for *Stenostoma tenuicauda*. These are much smaller, varying somewhat but about one-half the size of the above and are more numerous, showing about three times as many in each individual. They are quite flat against the surface and protrude only slightly, while those of *Stenostoma tenuicauda* are heavier and nearly globular. These glands are undoubtedly digestive in function but their exact working has not been made out.

Other details of specific value are the special sensory organs. The ciliated pits on either side of the anterior lappet portion are small and shallow compared with those of *Stenostoma leucops* or *Stenostoma tenuicauda*. They are very near the end, half as far from the tip as the width at that point. They are not so conspicuous as in most species, since the epithelium is not thick or the cilia long and consequently the outlines are dim. The patelliform or light-refracting organs, on the contrary, are very distinct and appear as rather large, bright, almost iridescent spots directly back of the two sensory pits and on a line with the anterior edge of the mouth. They are not exactly round but have a slightly angular outline, showing thru the clear parenchyma, almost like two bright eyes. The size and brilliancy of these organs distinguishes them from the small dull structures in other species.

The zooid formation is another trait. The first fission plane is far posterior, cutting off about one-third of the body length. Second and third divisions are seldom found. The diameter externally is not changed until the internal parts have been nearly completed. The parenchyma acts as a protective cushion surrounding the partially developed brain and pharynx and at the same time confines and pushes back the intestine until only a very attenuated portion connects with the anterior zooid.

The distinctive details may be summarized as: first, slender glandular bodies occurring in the wall of the intestine; second, especially large and clear patelliform bodies together with small sensory pits; third, an extremely constricted connection betweeen pharynx and intestine; fourth, a cushion-like mass of parenchyma protecting the anterior end of the second zooid; fifth, the very regular cylindrical shape.

Family Microstomidae

This family name was proposed in 1907 by Alex. Luther to contain two sub-families, the Microstominae and the Macrostominae. Microstoma was before this time a genus of the Catenulidae, but the researches of Sekera (1888) and Vejdovsky (1895) and especially of Luther himself made a new classification necessary. The Macrostominae had been a group composed of three genera. The interrelation of these two sub-families was made on the basis of the

paired excretory tubules, simple pharynx, and ventral mouth. The main differentiating characters are: first, the presence or absence of a preoral intestinal diverticulum; second, the habit of asexual budding possessed by the Microstominae to a surprising degree, and not present at all in the second group.

Microstoma caudatum Leidy 1852

Figures 52, 53, and 56

The Microstominae contain two genera, one of which is found in this country, four species having been reported from one or two places in New York and Michigan. One of these, *Microstoma caudatum*, is present in large numbers in an artificial pond at Grinnell, Iowa. It has been taken as late as the last of November from heavy masses of Cladophora floating near the shore, and to the naked eye appears very much like *Stenostoma leucops*, which was also to be found in some parts of the pond. Almost all of the specimens showed three distinct fission planes, two nearly complete pharyngeal cavities, and two others at a much earlier stage of development.

This was clearly *Microstoma caudatum* but in several minor points it differed from the original descriptions of that species. In size it was about two millimeters long, the averages of the whole number of specimens taken varying within very narrow limits. The anterior end was not as large and round as the eastern type. It seemed slightly pointed at the apex, being very little broader than the posterior tail end. The tail part also was somewhat different from that of the original type in that it was round and blunt and not at all pointed. The whole surface was smooth and regular, showing almost no indentations at the lines of fission. The color was a very transparent, almost iridescent, pale, yellowish-green. The intestine when empty was also surprisingly clear, showing hardly any yellow at all, blending with the surrounding parenchyma. There was the greatest difference, however, when it was more or less filled with food material, as then the color was a distinct gray giving an entirely different tinge to the body as a whole.

The epithelium is very thin and transparent but bears extremely long cilia which are few in number, of the same size all over the body, and rather heavy. The most noteworthy details of structure are the nematocysts, which are very conspicuous and correspond to those of the hydra. They are nearly one-third as large as the pharynx and are spherical in shape. Before being discharged, they appear to have a small, sharply-tipped cone-shaped structure within and lie parallel to the surface of the body. When the cell is set off, the thread of the sting is shot out from the tip of the cone. These nematocysts are scattered very evenly over the body, and are about fifty or sixty in number.

The muscular system is very slightly developed and together with the parenchyma forms only a small part of the body make-up. The pharynx is deep and broad, cup-shaped, with the mouth opening very large. When closed, however, the mouth makes only a narrow slit on the ventral side, standing

out sharply against the circle of the pharynx. The intestine is broad, its diameter being very little less than that of the body; the wall is well marked and solid. It is not an even cylinder but shows a tendency to widen at each fission plane. This brief summary emphasizes the many minor variations which may be evolved in different environments.

Macrostoma sensitivum Silliman 1884

One individual of this species was taken from a small pond in which seven other rhabdocoels occurred in larger or smaller numbers. In most respects it agreed very closely with Silliman's description but in regard to a few points, added details may be of value. The rhabdites which are arranged in groups of two or several, lie in large, spherical cells. In shape, these rods are long and straight, rounded at one end and somewhat pointed at the other. Generally, tho not always, they lie parallel to each other. The rhabdite-bearing cells are scattered evenly over the surface of the body and not at all gathered into tracts. In the cytoplasm there are a number of large, light colored globules, placed in close proximity to the rhabdites. These globules are relatively large and prominent and evidently have to do with the functioning of the cell, tho whether they are stored nutriment or are merely a by-product of the heavy metabolism is not clear.

The sensory organs are also noticeable. The eyes are very far apart, nearer the lateral margin than the middle line of the head. The sensory hairs are clear, sharply pointed and seem often to be bent back at right angles to about the middle. This bending may be directly opposite to the position of the cilia, a fact which seems almost impossible. In general these hairs are evenly distributed, but sometimes they may be grouped in tufts of six or eight.

The digestive system as a whole varies not at all from the eastern type but the muscular power of the pharynx seems extraordinarily developed. The mouth with its boundary of heavy glandular cells may be protruded as a cone-shaped elevation which is constantly being turned from side to side. The muscular development extends back thru one-fifth the length of the intestine and is very conspicuous in the live animal.

The reproductive organs are also noteworthy. The chitinous portion of the copulatory apparatus is bent, as usual, but the whole tip is broader and heavier than in the original diagrams. The eggs develop, a number at a time and crowd forward, stretching the oviduct and filling the space between the intestine and the body-wall. This brief summary covers the main details of variation.

Macrostoma album nov. spec.
Figure 21

Of the three genera which make up the family Macrostomidae, only one is represented in the eastern states. Two species, *Macrostoma appendiculatum* O. Fabricus and *Macrostoma sensitivum* Silliman have been found, as a few specimens at two or three different times in this study. The former has also been taken at Lincoln, Nebraska, and thus the distribution appears wide-spread.

Several specimens of another species have been found in the same pond with Strongylostoma. Superficially, they appear like large Stenostoma, except that they are a more opaque white and are never seen swimming free in the water but crawling over the surface of the aquarium, hunching along, as it were, one part of the body at a time. The movement is slow and uneven, with great difficulty, by means of muscular contractions, slight waves passing over the body very slowly. When at rest, the animal lies crouched and somewhat drawn up with the head bent a little to one side and more or less of another little bend at some other point. When in motion, the head is hardly ever held straight with the body, but is constantly moved this way and that, as tho investigating the surrounding surface.

In size the individuals vary from 0.75 to 2.1 mm. in length, the measurements taken when the animal is as extended as possible. The width was hard to ascertain because of its great amount of variation, never being the same for any length of time. The average was 0.3 to 0.7 mm. for a point about the middle of the body. The depth was nearly that of the width except in the tail region, where there was some flattening. As a whole the animal is very nearly cylindrical. The head end is as broad as any part of the whole body, but very amenable to change, so that often it appears pointed. In a lateral view it shows a slope to the ventral surface, making a blunt point. At about the region of the eyes, nearly one-fourth of the body distance back from the anterior tip, there is a very slight constriction, which is gradual in slope and does not appear unless the animal is quiet and fully extended. Posterior to this the body diameters are very nearly the same as far back as the last one-fourth, where there is a gradual and even narrowing toward the truncated tail. The ventral surface is somewhat flat, but the lateral surfaces very gradually round upward so that there is only a very narrow, entirely bottom surface. Color seems to be lacking. The opacity apparent to the naked eye disappears under the microscope, showing only a very transparent body. Even the outline is not as definite and clear-cut as in many other white forms. The intestine shows somewhat darker than the clearest portions but the outline is almost invisible. The eggs alone are dark and thick, but have no especial color. The atrium seminalis and sexual pore are very gray-orange with smooth walls distinguishable from the cellular parenchyma. This parenchyma gives a pale greenish tinge to the body as a whole.

The epithelium is thin and clear, the cell outlines hardly visible and even the inner margin not distinct. It is of nearly even thickness over the body except on the ventral surface of the tail where it is made heavier by cells specialized as a holdfast. There is no such highly developed point on the head, since the animal nearly always holds the anterior end a little elevated, preventing any contact with the substratum. The rhabdites are very inconspicuous, being small, regular in shape, and clear. They are straight rods scattered thruout the integument, to some little extent grouped together in threes or fours but generally lying in various positions, except never end to end. The cilia

are fine and are in length about the thickness of the epithelium. They are distributed evenly over the surface of the body. Their movement is regular and gentle with no heavy waves of motion. This lack of power is to be correlated with the crawling rather than the swimming habit, and also with the strong muscular contraction which causes a large amount of bodily twisting and turning. There is never the smooth gliding motion so characteristic of types propelled by ciliary motion. The tail portion alone has specialized cilia. Over the upper surface and to some extent down on the ventral side there are cilia which are about four times the size of those of the rest of the body. They are from twenty to thirty in number and rather irregularly placed, standing out stiff and spine-like in all directions. They do not flex and wave as do the others but are more rigid, thicker walled and conspicuous. They are sharply pointed with somewhat broad, heavy bases, and are evidently sensory in function. With this exception the integumental details appear specialized to only a small degree.

The muscular system is important. The muscles are many cells or fibers running in a more or less longitudinal direction altho often somewhat oblique. These connect the anterior regions with the posterior end and are the principal source of locomotive power. The muscles which control the action of the head are stronger on the dorsal side and run in a number of directions, interlacing to form a network strong enough to lift the bulky head. The action of the pharynx is also heavy and forceful; in fact this is one of the most muscular species. But with all this power of contraction, the muscle strands are still so delicate as to be very nearly invisible. They are never concentrated as to be at all solid or firm, but are rather single cells depending for their strength upon the sum of all their work.

The parenchyma is visible as a transparent material making nearly one-half the body mass. It is almost the whole of the large head and extends back completely surrounding the intestine and reproductive organs, even filling the broad tail region. The cellular structure is evident even tho its extreme delicacy makes it appear almost a cobweb. The cells have several long, irregular processes, running in all directions, making a network much like that of other forms but less heavy.

The digestive system is thin-walled and in all specimens very nearly as transparent as the parenchyma. Its boundary is somewhat irregular and the elasticity or limit of extension less than in many species. The pharynx is nothing more than the narrowing of the anterior end of the intestinal cavity to the mouth region. It is not at all marked off from the rest of the digestive tract so that its limits cannot be distinguished. The mouth when closed is a thin slit just posterior to the eyes, when open it is triangular or roundish in shape, the wider part being anterior. The bounding wall around the mouth is heavy, about twice the thickness of the integument. It is well-defined and shows the muscle strands which control it. The intestine itself extends far back into the tail region but not much farther forward than the mouth. The

cells which make up the wall are rather large, and squamous-like, but their boundaries are not heavy enough to be clearly distinguishable. They do not show the large oil globules found in many species and the protoplasmic content is much more fluid.

The nervous system consists of an angular brain ganglion upon whose surface the eyes are placed. This is about one-fourth the body length from the anterior end and leaves a broad undifferentiated space before it, a detail which recalls the like condition in *Macrostoma sensitivum*. The eyes are dark, very small crescents, placed near together. The diminutive size together with intensity of color, which causes them to be conspicuous against a light background, calls attention to them. There seem to be no other especially developed sense organs, which is not surprising in an animal so sluggish in movement and so lacking in definite reactions.

The reproductive organs are conspicuous because of their opaque grayness and consequent visibility. The testes are distinctly dull colored and extend from the ventral posterior region up around and forward, partially clasping the intestine. The ovaries are just back of the testes on either side. This form differs from others of the genus in that eggs develop in two diverticula of the ovarian ducts. The diverticula are simply expansions of the ovarian wall and its duct and with the enlargement of several consecutive eggs they push forward to a point only a little posterior to the mouth. A number of eggs of various sizes will thus lie in a row on each side of the body, the largest posterior, down near the sexual pore and those farthest forward not more than one-half the size. The female genital pore is very large, situated about one-fifth the distance from the posterior end. It is irregular in shape, and with a thick wall. The male pore is slightly posterior and much smaller and thin-walled. The reproductive season is during January and February. Evidences of asexual budding were not present.

The general points of comparison with other species are briefly: first, differences in shape; the head is much longer than *Macrostoma sensitivum*, the tail much narrower than *Macrostoma appendiculatum*; second, the eyes are very small, much farther back and closer together than in either of the other two forms; third, the male chitinous spicules are shorter, more simple and not so sharply pointed. Other details in which the members of the group show some resemblance are the very light color, the large, hair-like cilia at the posterior end, the large mouth and comparatively simple intestinal cavity, the position of the ovaries, dorsal to the testes, and the generally spatulate tail.

A number of specimens of this species have appeared in the ponds near Havana, Illinois, and also at Urbana, showing that the distribution is fairly widespread thruout the state.

FAMILY PRORHYNCHIDAE

The family name Prorhynchidae was suggested in 1862 by Diesing for the one genus, Prorhynchus, at that time containing a single species, *Prorhynchus*

stagnalis, which had been described by M. Schultze in 1851 as a seemingly aberrant form. It possesses an armed proboscis-like structure so resembling the stinging apparatus of the Nemertinea that the early authors thought it must be an intermediate type. In 1885 von Graff pointed out that the so-called proboscis was merely the stylus of the copulatory organ situated far anterior, and that there were really no special characters to relate this species to the Nemertinea. Thus the integrity of the family was settled. Eight other species have been added to this genus but even yet the family remains the smallest of the Turbellarian group. The nine species are strikingly similar in a general way, the differentiating characters, however, being well-defined. Two species, *Prorhynchus stagnalis* and *Prorhynchus applanatus* have been found in the United States, the former in New York and in brackish water at Falmouth, Massachusetts, the latter in a greenhouse in Lincoln, Nebraska.

Prorhynchus stagnalis M. Schultze 1851

Several specimens of this species have been found in ponds at Urbana, Illinois. They were taken during the latter part of April, from the protected side of a mud-bottomed little lake. They came with the loose silt from a depth of three feet, where the water was fairly clear and containing little or no algae.

In a large aquarium of this same pond water, their actions were watched. Superficially, they resembled little white leeches, both as to general shape and the manner of retracting the whole body and then stretching it out quickly, the head free, the tail attached, searching in all directions. This motion is constant for lengths of time, the animal seeming almost frantic in the quick nervous motions. It crawls over the glass wall of the aquarium, covering quite a distance as it does not hold its course much of the time. It also creeps up and down the larger stems of Chara and other water plants, but never is free-swimming. All the movements are of the muscular type and are precise and quick. There is only a weak ciliary action which has little to do with the locomotion, since it is as heavy when the animal is quiet as when active. The power of contraction is well-developed, the animal often drawing up to one-fourth the extended length. The average when at rest is, however, between one-half and three-fourths the greatest extension. A noticeable fact is that when drawn up and quiet the width is not changed, the extra enlargement having its effect entirely upon the depth. When thus contracted, the head is not generally drawn nearly straight back up to the heavier part, but is more or less bent to one side so that the form is not compact but irregular.

The general appearance is striking and characteristic. In size, there is little variation, the length being very nearly 4 mm. and the width 5 mm. in any part of the body. The shape is noteworthy, being a regular oblong with only little change at any point and as a whole it is thin and flat, the only appreciable thickness being thru the intestinal region just posterior to the middle where the dorsal surface rounds up a little. At both anterior and posterior ends the

depth is exceedingly slight. The head is sharply truncate, square with the ciliated pits smaller than is reported for other forms. The posterior half of the body is much larger and darker than the European type, showing a greater contrast with the margin and with the head which is extremely transparent. The pear-shaped cells in the integument seem to be more conspicuous than is usual, as they are clearly outlined against the rest of the epithelium. Since there are very many, they are arranged close together. The parts of the structure appear clearly. A large outside portion made of a single cell with thick definite wall contains an eccentrically placed smaller part round and dark in color. This evidently bears some relation to the nematocysts and rhabdites of other species. These details are of some interest in showing the amount of variation in a single form.

Prorhynchus applanatus Kennel 1888

During the month of February, in collections from under the ice, individuals of this species appeared crawling in masses of Cladophora. This is a very different habitat with different environment from that of a greenhouse where it has been found before. The animal was noticeable on account of its pure white color and quick jerky movements as it crawled thru heavy tangles of alga or hurried over the side of the aquarium jar. In a few respects it differs from the type descriptions. The body is not more than 3mm. long when fully extended and about one-fifth as broad. It is extremely flat on the dorsal side, the arching over the intestine being slight. The shape as a whole is not so slender as in Kennel's drawings, being nearly an oblong with parallel sides and nearly parallel ends. The anterior surface is deeply notched at the point of the mouth opening, giving the two lateral corners an almost lobe-like appearance. This, with the clear transparency, makes the head-region conspicuous. The tail end is much more rounded and short than in other cases, which causes the whole body to seem broader. The color as a whole is a much denser and purer white than that of *Prorhynchus stagnalis*, showing a yellow tinge only over the intestine.

The pharynx shows clearly its division into heavy, large secondary cells which act as a support for the four pointed tooth-like cells which work in connection with each other and recall the Aristotle's lantern in the Echinoid. They are relatively large and muscular, occupying one-fifth the body length. The method of working is peculiar, as the movement is entirely confined to the narrow space within the pharyngeal wall. There is little expansion and the limits of motion are narrow. This is balanced by the drawing backward and forward of the whole structure which gives a purchase on whatever material is held at the mouth opening. The intestinal diverticula are large but very irregular and many are not straight but curved and bent. This differs from the extremely even condition in the original type.

One other detail might, perhaps, be mentioned, the small size of the eyes. They were of the same bright color but were not more than one-half the size given for the European specimens.

About the last of July a few individuals of this species were found in the overflow waters of the Illinois river. They were in every way more developed than the other specimens seen. The length was over 4mm., the color a glistening milk-white, the intestine rounded and standing out clearly, the whole animal having a well-fed appearance. The characteristic nervous movement was conspicuous. Under a very small stimulus, excited and almost terrorized actions were aroused. The rather peculiar waves of motion which pass over the body as it hunches along are to be noted in contrast to the smooth manner of most species. In this instance, the waves were very well marked especially at the anterior end, giving the animal when in motion a ridged or wrinkled surface, quite significant.

FAMILY DALYELLIIDAE

The Dalyelliidae have had an irregular history. Starting in 1843 with the descriptions of Oersted and continuing to the present time, this family has been the subject of many descriptive and systematic studies. Oersted named several species belonging to the genus Oerstoma and then proposed the family name Derostomeae. Schmidt (1848), Uljanin (1870), and Jensen (1871) worked over this family adding species and defining the genus characters as well as describing several genera belonging to other nearly related families. In 1882 von Graff reclassified the whole group, incorporating with Derostoma the old genus Vortex Ehrenberg (1831) and naming the family Vorticiidae from the latter genus. He created two subfamilies to contain the eight genera. Then, later, in 1903, he again renamed the Vorticiidae, making a family, Dalyelliidae, with two sub-families, the Graffillinae and the Dalyelliinae named after the two oldest genera, respectively, and at this time also because Vortex had been used in 1797 for another form, he substituted the name Dalyellia first used by Fleming in 1822 for that genus. Again in 1908 on the basis of a paired ovary he made two families the Graffillidae with two ovaries and the Dalyelliidae with only one. The latter family was made to contain six genera and sixty-one species, all European forms. Before 1911 three or four species had been identified for this country, all new. In his paper of that year von Graff described eleven others, most of them taken from the locality around Rochester, N. Y. Thus the present conception of the family is quite different from the early orignal description.

The more general distinguishing details are the presence of a single ovary and two yolk glands, a simple genital pore, and the anterior barrel-shaped pharynx without a sheath.

The pharynx is the most conspicuous detail of structure. It is often slender and long, often short and nearly spherical, but generally the checkered appearance of the wall is well-developed. It is always of relatively large size and holds its shape constantly, not being at all collapsible. It is thus very sharply marked off from the intestine which is of very different structure. During the reproductive season the vitelline glands running forward on each side of

the intestine are very prominent. The ovary, testes, and other accessory parts are often so embedded as to be difficult to make out, but always the yolk glands can be seen nearly as large as the intestine itself, extending up around it toward the dorsal side. In many instances also the rather large opaque egg is evident, more or less completely filling the posterior region of the body. The anterior end is commonly truncate with the mouth a conspicuous hole just ventral to the very front margin. The development of a tail-like portion is somewhat variable but all the forms show at least a tendency in that direction. The shape as a whole is much more slender than in many families. The color ranges from almost black to clear transparency. The above summary mentions points in the general make-up which causes this group to be one of the most easily recognized of all the families.

Dalyellia dodgei von Graff 1911
Figure 49

This species was taken together with half-a-dozen other rhabdocoels from a small temporary pond which during April was up to four feet deep but which later would dry completely unless the rains were especially heavy. It drained down into a little river and so was not entirely cut off from the outside. There was a muddy bottom with some algae and many leaves from near-by oak trees. The site was protected from wind by hills so that the warmth of the sun was felt early. The special locality was the surface of bottom mud or a small mass of algae. Either was a good hiding place as the animal is nearly black. The motions are sluggish and not constant. When at rest, the body is drawn up to one-half its extended length and seems almost round. It is not as easily frightened as most of the other species and when aroused more quickly becomes quiet. One little habit is quite noticeable. Very often when the rather small mouth is opened, the front end of the head is slightly elevated to give the ventrally placed mouth cavity a more advantageous position. The two corners of the head are very contractile and are used almost like lips to guide particles of food into the opening between them. When the animal is moving along, the mouth is closed and the ventral surface held down. The head never turns from side to side, and the whole body is straight, keeping to a rather definite course for the most part.

This form agrees closely with that from Rochester described by von Graff. He speaks of it as occurring there more frequently than almost any of the other rhabdocoels. The conspicuous characters are: first, double arrangement of the pharynx with its especially developed papillae; second, the mottled color due to scattered pigment cells, and third, the complexity of the reproductive organs. This western type is noteworthy as showing wide distribution in a species found commonly in a certain restricted locality, and seems to be indicative of its probably wide-spread occurrence. A resume of its variations may be of interest.

In size and shape my specimens are very nearly those of the eastern form but the color is strikingly different. Altho showing a sepia-brown when the animal is compressed to such an extent that the parenchyma is a thin layer, yet under ordinary conditions it is very dark. It appears evident that the pigment cells when fully developed lie so close together as to aggregate in a color nearly black. It is really a dull brownish-black, so opaque as to obscure entirely the internal organs. On account of this color in the parenchyma, the integument by contrast is exceedingly prominent. It is especially thick and possesses an almost iridescent transparency. It so reflects the light as to show the convexity of the body surface. This gives an appearance of solidity not present in most specimens. The cilia are fine, clear, and very swift and heavy in their motion, as a result of the lack of a strongly functional muscular system. The parenchyma is composed almost entirely of pigment-bearing cells. That is, there is no layer of colored cells on the outside just beneath the integument as is commonly the case, but most of the parenchyma cells contain more or less pigment substance so that the color is scattered. The fluid material is present but it is not conspicuous. In shape, the cells are irregular and in most respects they resemble the parenchyma of other forms. The digestive tract is different from the type only in minor details. So covered by the pigment that it is not apparent until crushed out from the surrounding tissues, it shows the characteristic green of the wall cells. The pharynx apparatus is especially long, extending back thru more than one-third the body length. The anterior vestibular portion is shorter than the pharynx proper, but is of about the same diameter. The papillae on the surface of the vestibule are very slender and lie far apart.

The only point of note in regard to the reproductive organs is the duct leading from the uterus to the genital pore. This is extremely slender and long, a mere thread reaching up into the body mass for a distance almost equalling the main diameter. In specimens where the egg is very large and ready to be laid, the duct appears almost incapable of such extension as must be necessary. The yolk glands, testes, and ovary lie embedded in the parenchyma.

It seems probably that this species feeds upon the minute algal growths in the filamentous masses where it habitually lives or upon plant debris just below on the surface of the mud. It presents a type of structural detail very different from most other species.

Dalyellia alba nov. spec.

Figures 24 and 26

The habitat of this species presents conditions very nearly like those of most ponds. A muddy bottom, with roily dark water, some amount of leaves and other organic debris and much floating Cladophora make a surrounding environment suitable for rhabdocoel types. Chief among these is *Stenostoma leucops*. The Dalyellias are always taken from masses of algae. They appear

to find in such a situation both a good feeding ground and a safe lurking place. In very many hauls a few specimens appeared, but they were never in such numbers as Stenostoma and were never so boldly free-swimming. They are often seen, however, gliding out from mazes of filament and seem to swim partly by ciliar action and partly by muscular contraction. They spend most of the time clinging or crawling among the algae but when removed to a watch glass or aquarium never seemed to creep over the surface as do other species. That is, their organs of attachment are not developed and the locomotion is entirely free.

The general appearance much resembles a short, heavy Stenostoma. The length varies from 0.75 to 1 mm. but seems much less owing to the relatively great width. The width is about one-fourth the total length except in the posterior third, which is narrowed as a tail portion The depth varies at about the same rate as the width and is always very nearly the same for any given part. That is, the ventral surface is convex with no flattening. The twisting and contraction are only slightly developed, altho the body is not as rigid as is the case in many forms and the head is often drawn in, the back humped up and the whole made into a nearly perfect sphere. Superficially, the color is an opaque-white with a slight greenish tinge which is heavy enough to make the animals stand out prominently. There seems to be no pigment whatever, even the eyes are not brilliant or dark as in most members of the genus.

Both integument and parenchyma are somewhat clear. The former is thin and regular in outline, allowing the scattered rhabdites of the internal layer to show thru. The cilia are quite definitely heavy and regular all over the surface except on the tail, where they are about five times as large. The whole end portion of the tail region is evenly clothed with these larger cilia, making a specialized organ of locomotion. The layers of tissue beneath the skin are masses at either end of the body, and also form a thin envelope over the central body organs. This parenchyma is very closely meshed containing space for only a very small amount of fluid material, so that the appearance of both the head and tail is as thick and dark as the middle part. This is somewhat unusual, as the extremities are almost always nearly transparent. Another point to be considered is the fact that these two ends are of much greater relative size than is ordinarily the case. This seems the result of the storage or concentration there of so much undifferentiated tissue.

The central body mass is almost entirely composed of the digestive and reproductive organs, the latter during the reproductive season occupying most of the space. The pharynx and intestine are typically simple. The mouth is ventral, lying just posterior to the eyes and opening into the heavily-walled pharynx which is cask-shaped but very narrow in front. The boundary of this rather muscular structure is sharply defined and reflects the light to such an extent as to appear glistening. It is comparatively small and not more than one-sixth the body diameter. It opens directly into the intestine proper, which is thin-walled and dark. This extends back to the genital pore. During

March and April, the intestine is more or less obscured by the large yolk glands which extend forward as far as the eyes. These are heavily lobed but when fully developed become compact with a very thin dividing wall. Overlapping the posterior third on each side is the testis, very finely granular but much lighter in color. The ovary is small, posterior in position and well embedded in the parenchyma. The eggs which have a diameter about one-fourth that of the body, are thin-shelled and gray in color. They pass the embryological stages in the uterus lying near the middle or a little to one side in close proximity to the genital pore which is very large. As a whole the reproductive system is conspicuous.

The most noteworthy details of structure may be summarized as: first, a broad head and tail region with a large amount of parenchyma tissue; second, a small pharynx, and third, large yolk-glands.

Dalyellia megacephala nov. spec.
Figures 23, 25 and 39

The situation in which this species is found is of typical formation, the important details being a muddy bottom, a small amount of algae, and a large animal community. The general appearance is striking, due especially to the relatively large eyes and pointed head. The length is about 0.75 mm. the width 0.2 to 0.25 mm. and the depth somewhat varying but never more than the width. In shape the animal very closely resembles many others of the same general type. The anterior end is bluntly pointed and flat. The middle region of the body is rounded out, being plump and much thicker than the rest. Then the posterior end is slightly attenuated and more pointed than the head but cylindrical instead of flat. There is really no color but to the naked eye the whiteness is opaque flecked with the black spots of eyes which are large enough to be easily seen.

The integument is conspicuous, since its boundaries are definite and clear cut. Here again the inner wall is heavy. The cilia are very short and fine, all of about the same size and evenly distributed over the body. The rhabdites are not gathered in special tracts but are scattered thruout the inner portions of the epithelial cells. The arrangement is quite lattice-like in its regularity, the small groups of straight rods lying at right angles to each other.

The muscular system is heavier than in many forms, as much of the locomotion is effected by means of body contraction. It lies, however, very near the integument, a condition which is partly due to the fact that the parenchyma is not abundantly developed. The lack of parenchyma seems to be correlated with the relatively large digestive system, which nearly fills the body mass. The pharynx is very large and extends far forward leaving anterior to it only a small triangular area. The wall of the pharynx is made up of two kinds of cells, regularly placed. Those lying longitudinally are very slender and reach the whole length of the organ. Those extending around are also narrow and thread-like, and together with the longitudinal cells make a cross-hatching

in the interstices of which are large, broad cells acting as a framework. The whole is very muscular and is turned and moved constantly. The position of the mouth is noticeable. When closed, it is a very short slit at the anterior ventral edge of the pharynx. When fully open, however, the posterior corner is drawn back ventrally as far as the connection with the intestine making the whole pharynx bend downward. The opening itself is very large and conspicuous. The intestinal wall is rather heavy but otherwise the details of structure are not strikingly different from other species of the genus. The food is to some extent at least, composed of the eggs of other forms. In the intestine of one specimen, eleven eggs of *Typhloplana viridata* were found. It was possibly true that these all come from a single individual which had been swallowed bodily and the soft parts quickly digested. The heavy muscular development together with such food masses seem to indicate a habit of voracious feeding.

The reproductive system is extraordinarily far forward with the single genital pore nearly at the middle of the body. The two testes are long, slender organs opening by a complicated sac-like apparatus into the receptaculum. The head portion of the spermatozoon is very large and is easily distinguished on thru the wall of the vesicle. The ovary lies a little to one side of the middle and carries about ten eggs. In the younger stages it exhibits very many small iridescent globules arranged in rows along the edges, where the eggs touched each other. When the eggs leave the ovary, they pass down the short oviduct to the uterus where, one at a time, they develop until they have a diameter one-fourth that of the body. At maturity the egg is very conspicuous because of its heavy wall and solid yolk mass, showing thru even the thickest portion of the body mass.

Altogether this species possesses rather notable individual characters.

Six other species belonging to this family have been seen at different times, but have not as yet been completely identified or described. The family is very common in ponds both north and south.

FAMILY TYPHLOPLANIDAE

In 1831 Ehrenberg used the name Typhloplana for one of the twelve genera which he described at that time as making up the new class Turbellaria. Five years later he described the genus Mesostoma, which gave the family name used until 1905, when von Graff outlined the general characters and gave the distinguishing limits to the group. He then proposed the name Typhloplanidae from the oldest genus of Ehrenberg, for this new family, which included only the old Eumesostomina and a few new genera described by Luther (1904). The other parts of the Mesostominae Dugès were made separate families. The Typhloplanidae stand now as composed of three tribes, as suggested by Luther, having two, six, and two genera respectively. Of all the Turbellaria, this family is the best known. As von Graff says, the histological work of Luther and the descriptive work of several other writers have made possible a really clear understanding of their morphology and biology.

In the United States, nine species belonging to this family have been identified. All are from localities in New York except two, *Bothromesostoma personatum* and *Mesostoma ehrenbergii*, which have been found in Michigan and Illinois. To this list may be added several others.

Rhynchomesostoma rostratum (Müller) 1774

This is, perhaps, the most delicate of all the rhabdocoels. One of the very first to be described, it has appeared again and again in many places. It is naturally a northern form and is found in cold water, under the ice or early in the spring. Von Graff had specimens from a peat bog in Rochester, which measured only 2 mm. Those which I have had come from a small temporary pond having a muddy bottom which was covered with dead leaves, sticks and a little algal growth. The water is never clear and was in the process of drying up. The length is in every instance more than 2 mm. and a few individuals measure 3 mm. All, however, are slender when extended with the anterior and posterior ends drawn out to very long, sharply pointed tips. The whole body makes a very regular spindle with the pharynx protruding only slightly on the rounded ventral side. The proboscis like head is more conspicuous in its contraction than that of the European forms, for it can be drawn back into the body as far as a point even with the pharynx, thus making the anterior end of the greatest width. The two transverse rings of muscle attachment are to be clearly seen. A condition opposite to this is found in the tail which is not at all retractile. The color is another noteworthy character. Since the integument is exceedingly transparent, the internal parts are easily distinguishable. The parenchyma in all my specimens is of a clear, pale rose, without the slightest tinge of yellow. Within this the intestine and reproductive organs show definite outlines. The wall of the intestine is somewhat gray, with very small cells which are nearly all of the same size. Scattered among these are bright carmine red oil globules of about double the size of the other cells and evenly distributed over the outer layer of the digestive tract wall. These help to add to the general reddish color. Of the reproductive organs, the ovary, testes, and atrium are grayish with clear, sharp walls, and are not conspicuous. On the other hand, the developing eggs and vitelline glands are of a deep, brilliant red. The glands are compact with irregular lobed margins. They are about one-tenth the total length of the body and lie near the surface on each side at about the middle. They vary in size but not in intensity of color, reaching down to their connection with the atrium as only a very narrow thread. The eggs, either one or two, are matured in the atrium which forms a sort of egg capsule. The color is lodged in the tough, thick shell which is withal sufficiently transparent to show the yolk granules within. These yolk granules when removed from the shell are white and clear, of somewhat varying size. One set of eight eggs measured showed diameters varying from 229μ to 288μ. They were very nearly spherical, two diameters in a single egg generally differing not more than 5μ. They lay just behind the

pharynx in the heaviest part of the body and were visible even to the naked eye. The specimens taken during April were all carrying eggs which generally were extruded. As the animals lived isolated in watch glasses, it was easy to keep track of them. The first developmental stages were carried thru but most of the eggs died before the second cleavage.

This mud-loving form is, of all the Turbellaria, the most ethereal; it is daintily tinged, a mere transparent shadow against the dark background.

Strongylostoma rosaceum nov. spec.

Figures 1 to 20, 28, and 54

Specimens were first seen during the early part of November in the ponds at the United States Biological Station at Fairport, Iowa. They appeared together with other rhabdocoel species, both swimming free in the water and also coming out from masses of algae and water weed which were dragged up from the sides and bottom of the ponds. They were present in larger or smaller numbers in all the collections made during the next three months. Individuals of this species were easily recognized by the rapidity of their movements thru the water and by their habit of launching out openly rather than crawling over the sides of the aquarium or on the plants. Altho frequent in most of the ponds and the reservoir which supplied them, in certain places where conditions seemed especially favorable they were exceedingly abundant. Such conditions appeared, in general, to be a large amount of filamentous algae rather than the coarser water weeds, a depth of water of not more than eight feet, and as might perhaps seem reasonable the presence of only a few fish.

These forms are of especial interest for several reasons. Both color and preciseness of structural plan are striking in intensity and definiteness. Among the more common rhabdocoels the color is nearly lacking or at least dull and varying with the surrounding conditions from a transparent white to an opaque gray-green. In comparison with such fresh-water types, these specimens are gorgeous, for even altho obscured by muddy water the clear delicate pink is noteworthy, and makes them stand out sharply against the greenish background, easily distinguishable from all other animal species. While most rhabdocoels and even many turbellaria are fairly simple structurally, in these the several organic systems are clear-cut and more completely developed.

Tho occurring in large numbers in these special ponds, they have not been found in other ponds in this region, and members of this same genus have been reported from only three localities in this country. Altho they are probably present in many places and will be found at some future time, they are evidently not at all commonly found in the fresh water mud-holes of the Mississippi valley.

The facts, that in water under the ice the number of individuals is large, and that the period of sexual maturity is mid-winter, may be correlated with the northern habitat of related species. In a number of rather widely separated regions in northern Europe, members of this genus have been described, and taken altogether this seems to be a cold water loving form.

Specimens were taken from the ponds in pails of water in the common way and then, one by one, removed with a pipette to small watch glasses or to a slide. For study alive, they withstand the presence of the cover glass better than other forms, since they do not easily or quickly break. Quince-seed jelly is not practical as only an extremely thick solution has any effect on the strong muscular movements. The best method is perhaps to quiet them with solutions of cocaine and chloretone. They are very resistant to anything of this sort and it requires large doses to produce a condition of quiet, and then disintegration is likely to begin in a comparatively short time. When the animals are to be killed, corrosive acetic or cold corrosive solution used directly after they have become quiet under the anesthetic will cause little contraction. They can then be stained, cleared and mounted in toto, and most of the organs will be fairly distinct. Sections were cut from four to eight micra in thickness and were stained in Ehrlich's hematoxylin and erythrosin.

The length was taken when the animal was at the point of greatest extension or at least when moving unhampered freely thru the water, so that both anterior and posterior tips were drawn out to acute points. A number of very small individuals were considered juveniles and not merely shrunken in size, due to lack of food. This seemed to be the case, since under starvation conditions there is very little shrinkage of body size, most of the change being in relative amount of bulging in the intestinal wall. Those specimens apparently adult will vary from 1 to 2 mm. in length, the average being within rather narrow limits, 1.3 to 1.6mm. The width is perhaps a little more difficult to compute, since it varies with physiological conditions, i.e., it depends upon the amount of food recently taken in and also stage of development of the reproductive organs. The limits of variation here are from 0.1 to 0.35 mm, the average being 0.2 to 0.35 mm. The greatest depth is very nearly the same as the greatest width, for altho the ventral surface is flat and the anterior part low, the portion of the body posterior to the middle is much elevated so that it is nearly cylindrical. Both the measurements of width and depth were taken at a point slightly posterior to the pharynx.

The amounts of expansion and contraction are very great so that measurements mean little except in a general way. A significant detail with respect to shape is the amount of food in the intestine, or at least the abundance of food at previous times. This correlation of nourishment supply with shape variation is the result of the flexibility of the assimilative cells. Under starvation conditions they are very minute and occupy no appreciable space in the body structure. When, however, the digestive sac is distended with nutrient material, these cells enlarge from five to ten times, and give the characteristic plump appearance to the animal as a whole. This species is especially contractile, so that it is able very quickly to accommodate itself to its surroundings. Under the slightest disturbance or fright it may be drawn into an almost perfect sphere, the tips of the head and tail being only the merest knob-like projections on the surface. The limits of extension are very much narrower

since there is almost no elongation possible and the animal, when moving, is always at its greatest length. All the changes in shape are more marked in the posterior middle part than anywhere else, the head almost constantly keeping its form. The term 'head' is used since the anterior third of the body is conspicuously divided from the rest by a somewhat narrower neck-like portion. The head, itself, is rather sharply pointed in front, the angle made being about forty-five degrees. A little farther back, on each side, the outline angles again forming two rather knob-like protuberances which are just a little in front of the eyes. Back of the eyes the neck constriction begins. This is merely a curving in of the body wall, which soon begins gradually to bend outward again. As far back as the middle line (a point immediately posterior to the pharynx) the largest diameter is reached, giving an appearance of general plumpness. The posterior one-fourth narrows back rapidly to a slightly blunt point. Altogether, the shape is rather short and broad, with a triangular anterior end and a pointed posterior tip.

The color, which has already been given as a delicate pink, varies from a pale rose to a deep terra-cotta, but is always of surprising brilliancy. This is apparent even to the naked eye, as is also the fact that it is only the posterior part which bears the color, while the head region is white. Usually it is the case that in most rhabdocoels there is very little if any tinge of color, since the epidermis is not at all pigmented. Such a characteristic condition of the integument is found here, also, and the special rose tint is lodged in another tissue. As a result of metabolic processes there is produced a very clear, light reddish-orange oil, which, in the shape of globules, is stored in the outside layer of the digestive tract wall and, owing to the transparency of the epidermis, is distinctly visible. For this reason that part of the body in which the intestine is situated is also that which is highly colored, while the anterior end, into which it does not extend, remains clear. The variable condition of the digestive wall as a result of more or less plentiful sources of food, causes very evident changes in color and also in the limits to which the color extends. Consequently, when the lobes of the alimentary tract are fully extended and reach far anterior, there will be some tint even in the head or, if there has been little or no food taken in for some time, then the whole animal will appear very light or almost white. Thus the color is in reality a by-product of the organic processes rather than of especial intrinsic significance.

EPITHELIUM

The integument is made up of a single layer of high columnar cells, in some portions carrying rhabdites and with a covering of cilia on the exterior. As a whole, it is an epithelium of the type found generally in the Turbellaria and varies only in many minor details of appearance and structure.

These high columnar cells make the epidermis a conspicuous body wall, a fact which is surprising on account of the extreme delicacy of the structure. Altho there is no cuticular layer, the outer boundary is very clear and distinct.

This is due, not to thickness of material, but to compactness and a membrane-like toughness. The inner line of the epidermis is also well defined, tho not as dark and sharp as the outer border. It is reinforced by a very thin basement membrane which helps to make a firm base of attachment for the numerous strands of muscle cells. Since almost the whole of the muscular system is, to a greater or less extent, connected with the integument, this layer must be able to withstand the stress of very nearly every contraction. The middle part, between these two clear boundary walls, is very transparent, since the cross walls show but little, and for this reason the shape and size of the epithelial cells is difficult to ascertain. This fact offers some explanation for the ease and frequency with which the cells break apart. Most of the minor injuries to the worm are tearings or breakings of this layer, which seem as easily healed again. It is probably of great advantage that the cells, because of their very slight connection with each other, are able to repair an injury very quickly. Under conditions of injury when the tension is released either entirely or only on one side, the cells very quickly become spheres, showing conspicuously their primitive flexibility and lack of specialized form. This flexibility is imperative when there is taken into consideration the demands made upon the epithelium in the way of sudden contraction and expansion. There is an incessant and constant change in the amount of strain brought to bear upon a single cell or group of cells. For this reason, either in a small portion or in the whole layer the shape and thickness do not remain the same for any length of time and except when perfectly quiet the thickness is not the same for any two parts of the body. Under some pressure the high columnar cells become flat, almost scale-like, and the layers consequently very thin. In general the average thickness ranges from forty to one-hundred micra.

The external surface of the entire body is covered with a compact coat of cilia. These are distributed very evenly, not being grouped. There is also little variation in size as they are not longer or larger even at the tips of the head and tail. No sensory pits with large cilia are present and those cilia around the edge of the mouth are also of the same general dimension. In shape they are slender spines with the base slightly larger than the upper portion, which is drawn out to a long, fine point. The length averages near the epithelium thickness, with a diameter of three to six micra, and they appear as extremely fine transparent lines. The vibrations are rapid and altho generally the waves of motion are from anterior to posterior, yet upon occasion they may be reversed. Then in different portions the action may be at times entirely independent of the surrounding surface, continuing in some portions long after the main part of the animal has been killed.

Other structures included, or at least connected, with the integument are the rhabdites, which are arranged in two tracts in the anterior portion of the head. These tracts are symmetrical and are placed one on either side of the middle line in the dorsal part of the parenchyma. The anterior half of each group is a broad, fan-shaped portion which extends to the very tip of the head

and back and down on each side nearly to the level of the eyes. This central broad part as it runs posteriorly along the middle line toward the narrow neck-portion of the body becomes itself very slender, like the handle of a fan, and thus continues back between the eyes for a distance. Nearly the posterior third of the whole group becomes wider again to about one-half the width of the anterior fan, and bends outward away from the middle line, reaching almost to the sides of the body. The outer posterior edge is truncate and straight, parallel with the side of the body Another group of rhabdites much smaller than, and lying directly ventral to the dorsal division, runs backward at some distance ventral to the brain. It starts anteriorly near the tip of the head as a part of the dorsal fan-shaped group, and, bending ventrally, becomes very narrow just beneath the brain but broadens out again posterior to it. It ends abruptly under the extreme front end of the intestine. The rhabdites which make up these groups are arranged in strands of very regularly placed cells, each containing a cluster of rather large rods. In the anterior part there are from twelve to eighteen strands which narrow down to two or three, lying very close to one another thruout the middle division, then in the remainder of the group there are from five to six strands broadening out a little. Each strand is composed of from ten to thirty clusters of rods placed end to end so that the whole appears as a series of long lines.

The rhabdites or rods are surprisingly alike in size, shape, and color. The average length in adult specimens is twelve micra, while the width or diameter is about two micra. When released from pressure of the body, these measurements remained constant. The shape is a rather bluntly pointed spindle. Thruout most of the length the diameter of the rod is the same, giving it the appearance of a rather long cylindrical pencil. The two ends are about equally pointed and generally slightly curved or bent to fit the contour of the bundle. The color is almost a steel white, not at all transparent, but bright and clear, with the edge very distinct and black. They seem like bits of metallic rods sharp and hard, embedded in the most delicate tissue imaginable. There is always a rather constant number in each cell, eight, nine, or ten, lying very closely packed in a solid ovoidal mass. The cell, itself, is quite large so that the rods occupy only the center and are surrounded by a large space filled with very finely granular protoplasm. These rod-bearing cells are situated either in the epithelium itself or in the parenchyma just beneath, as tho they had been crowded there. The rods develop one at a time, right in the cell, being differentiated, as it were, from the protoplasm. In many instances the rods lay with their points toward the surface and under very slight pressure were discharged thru the outside wall, seemingly by internal force, literally puncturing the cell. If, by chance, any entirely escape from the epidermis into the surrounding water, so that all tension is removed, they immediately curl, sometimes tying a knot, and then spin around as they are swept away by the cilia-made currents of water. Even under slight disturbance in the body they

lose their straight position and appear more or less warped. Altogether the epithelium with its cilia and rhabdites is a very characteristic part of the body structure.

MUSCULAR SYSTEM

The muscular structure forms not a layer but a finely ramifying system of most delicate fibers radiating in all directions thru the body mass. The fibers extend from one part to another, intertwining and interlacing into a regular tangle which is complete enough in itself, if the rest of the body mass were taken away, to preserve almost a perfect outline of the body organs. One has only to watch the constant movement of many portions of the animal make-up to realize the existence of very many contractile fibers. Since the worm is very sensitive in every part of its structure, every part must be capable of quick response. Since the habitat makes it necessary to find a way in any jungle of water weed or debris, each individual must find it possible to wriggle thru any maze within which food and shelter lie.

The anterior end is, of course, the most sensitive region and, as a consequence, its musculature is well-developed, connecting the several head lobes with each other and with parts farther back. The muscle strands are extremely delicate slender threads, most of them ventral to the brain ganglia. A very few extend directly across from side to side, a few others are oblique, but by far the most run from the different parts of the head back to the intestine or to the integument of posterior parts. They might be described as clusters of fibers starting from some point in the main body region and spreading out fan-like for their insertion somewhere on the inner surface of the head integument. Since the head is very flat and there are few dorso-ventral strands, the whole complex forms a plate-like layer, very thin in front and becoming thicker toward the neck region.

The muscles of the posterior half for the most part run between the intestinal wall and the integument, anchoring and making both more firm. These are all rather short. Other strands run lengthwise or obliquely from one part of the outer wall to another, or from a posterior region of the intestine to more anterior parts of the integument. There are also a few fibers reaching from dorsal to ventral points. Taken altogether these groups of strands form a peripheral layer just beneath the skin.

On the ventral side of the worm most of the muscle cells are connected in some way with the pharynx or mouth and function as an apparatus for either drawing in or protruding the surface. The musculature of the pharynx itself is quite complex. There are comparatively heavy bands of fibers encircling both outer and inner edges of the rosette, while between the heavy petal-like cells very numerous more narrow strands diagonal back and forth. The circular bands act as sphincters and by the force of their contraction cause the pharynx to work as a rubber bulb exerting power sufficient to dislodge very solid particles of food material.

Connected with the reproductive system is a series of muscle cells having to do with the control of the atrial pore and the discharge of sperm and egg cells The atrial pore, situated at the tip of a papilla, is closed by the contraction of fibers lying near the ventral body surface. These are attached to the skin at one end and to the pharynx or neighboring structures at the other. In the walls of the reproductive organs themselves are flat thin layers of delicate muscle made up of many cells lying parallel to one another and acting together as a whole.

Thus the muscular system has to do with the functioning of the several organs or with the specialized reactions of the different parts, acting separately and independently of each other. In this species, it reaches a greater degree of contractility than is generally the case in other forms.

PARENCHYMA

Parenchyma, or mesenchyma as it is sometimes called, is the term used to designate the tissue, or rather mass of cells, which fills the interstices between the several organs. It forms, as it were, the packing for the important parts which are thus buried and cushioned, fairly secure against at least minor injuries.

The cells which compose the parenchyma are irregular and variable in appearance. Soft and extremely pliable, spherical when free, very angular when confined, they depend entirely upon surrounding conditions for shape. Since they are not limited to any part of the body space but accommodate themselves equally well to the large open portions of head and neck region or crowd into the infinitesimal cavities between intestinal cells, it is imperative that they be capable of very readily assuming any form. Correlated with such possibilities for variation is a very delicate and membranous cell wall. The nucleus is large tho so clear as to be impossible to distinguish from the protoplasm around it except in cells which have escaped into the surrounding water. The cytoplasm is thin, almost watery looking, and contains a few rather conspicuous granules, the whole structure being very simple.

In functioning this type of cell serves several purposes. It takes the place of a circulatory system acting as the conductor for transfer of food materials. As it is in more or less direct contact with all the groups of cells in the whole structure, it forms a basis of connection between the digestive tract and other regions. Where more highly specialized cells would preclude the possibility of such connection, these seem to be able to carry it on thru even a comparatively long series.

Another point of importance is the support which is given to the several body parts, the parenchyma acting in lieu of a skeletal system. Since there is not even a cuticula to give stiffness to the integument, and since none of the organs possess the necessary rigidity in themselves, the shape is maintained by internal pressure. The animal is, so to speak, inflated so that it can hold its

form, much as plant cells are made resistant by their turgidity. Then, too, the soft tissues are held in place and prevented from crowding one another so that their relative positions remain intact.

As well as serving for purposes of support, this most primitive of all the tissues also protects. It is very spongy, being capable of undergoing a great amount of compression, as for example when the animal squeezes thru extremely small openings or when it bends or twists so that some one portion of the body is subjected to especial strain. The great amount of elasticity is also noticeable and causes the shape to vary. Thus, when the intestine is large and its wall thick, or when, during the period of sexual maturity, the reproductive organs occupy a great amount of space, the parenchyma is so compressed as to seem almost lacking. On the other hand, when the digestive cavity is empty and shrunken the whole body mass appears to be composed of parenchyma, the cells of other sorts being insignificant in comparison. In the case of injury, also, this valuable layer plays the main part. Forming scar tissues and furnishing cells for regenerative purposes, it seems embryonic in its ability to develop in various directions. It seems not far from correct to sum up the foregoing characters by comparing the parenchyma with the embryonic tissue of other forms.

DIGESTIVE SYSTEM

The digestive system is more complex than that found in most of the other groups of this class. It consists of a very well-defined pharynx opening into a rather simply shaped, sac-like intestinal cavity which occupies the greater part of the body space. So conspicuous is the whole structure that the general appearance of the animal depends entirely upon physiological condition. While all the other tissues are transparent and clear, the alimentary tract alone shows heavy and dark, giving the only suggestion of solidity, and without it the individuals would seem altogether ephemeral.

Situated in the middle of the body on the ventral side is the pharynx, which viewed from above is a large, sharply marked rosette. It is in reality an inverted cone or funnel with the small round mouth at the tip, opening down. The rosette is never entirely flattened, but slopes upward and outward to its connection with the intestinal wall. This connection is made with the very outermost edge of the pharynx, just above the large circular muscle band already mentioned. The lower, mouth-end of the cone is held in place by its attachment with the epidermis and by means of various muscle strands which also anchor it to portions of the ventral surface. There is no sharp line of demarcation between the external epidermis and the epithelium lining the rosette, so that the mouth is bounded only by the circular sphincter muscle. The pharynx wall, itself, is thick and heavy, due mainly to the size of the petal-like cells which, together with muscles which control them, give the characteristic shape. There are from seven to ten of these wedge-shaped structures arranged with the smaller end pointing down toward the mouth.

They are very rigid and act as a series of jaws. In structure and general mode of action, this resembles the bulbous pharynx of the Prorhynchidae, where the rosette cells number only four. The general shape of the whole rosette is changed very quickly and the complexity of its action makes possible a wide range of feeding habits.

The intestine into which the pharynx opens broadly is comparatively thin-walled. This bounding wall which is very transparent and elastic is made up of one or two layers of cells which act as an absorptive surface and are subject to an enormous amount of variation in size. When there is little food material either in the main portion of the intestine or in some part of it, the wall draws in so that the cavity is entirely obliterated. This is brought about by the pressure of the surrounding parenchyma as well as by the compressibility of the lining cells. On the other hand, when there is need for greater amount of space in the alimentary tract, the wall is crowded out in all directions, portions of it compressing the muscle strands and other organs. The anterior end often reaches as far forward as the very tip of the head, pushing its way dorsal to the brain ganglion and the eyes.

The digestive processes are carried on by means of these simple cells in the lining wall. In some manner the food material is reduced to very minute clear globules which are often ejected as the result of slight pressure or other stimulus. These globules are absorbed, converted during the process into an oil, and stored as droplets in the outer layers of the intestinal wall. These droplets are extremely variable in size and color. Those found in an individual at any one time will range from many which are just visible to some one-third as large as the pharynx rosette. The color is always very clear, a brilliant yellow-pink or some shade much darker. Generally, all the globules in a single specimen are the same tint but there is the greatest difference among several individuals taken from the same very small aquarium jar.

These rather striking details in the structure of the digestive system are characteristic of this family and sharply mark it from all others.

NERVOUS SYSTEM

The nervous system contains fewer cells and a smaller bulk of protoplasm than any other part of the whole structure. The several tissues and organs are so arranged that they are very easily reached by means of a rather scant supply of nerve material. The kinds of stimuli received are few, as a consequence the receptive apparatus is not at all complex and the problems of correlation and response are solved without great difficulty. A rather high degree of sensitiveness in certain directions and the possibility of a precise response seem to have been achieved with a minimum of anatomical detail. As a result of such primitive plan, the nerve mass is not sharply marked off into separate divisions but appears as a very homogeneous, almost undifferentiated whole.

The main or central part of the nerve tissue is the brain ganglion which is situated near the anterior tip of the head, on a line with the widest place.

It thus lies near the middle of the head, between the main muscle strands and the eyes. There is a slight division into lobes which gives the appearance, at least, of a double structure, but as there is no suggestion of symmetrically arranged nerve branches or in fact no regularity of position or size of fiber, there is little to show a truly paired condition. The nerve cells are fairly large but show little detail of development. The ganglion contains, also, other cells, either for nourishment or support. These may be distinguished by the fact that they have no branches at all. It may, of course, be true that they later develop as true nerve cells. The nerve connections can hardly be said to be definite trunks or even special nerves since they seem almost like projections of the ganglion, amoeboid in their promiscuous wandering. Most of the fibers, or nerves, as they may be called provisionally, find their way to the skin, spreading out over the inner surface and forming a layer of receptive material. There are very few nerve strands extending toward the intestine and even the muscular system is poorly supplied. The greater part of the nerve mass is evidently sensory, and it seems the function of the motor nerves must be provided in some other way, perhaps by the direct responsiveness of the muscular tissue itself. Since there seem to be no cells purely associative in their activity, the various stimuli are probably passed from cell to cell. But however primitive the nerve tissue may appear, it very truly shows a great advance over that found in related families.

Closely connected with the nervous system and acting almost as a part of it, are three types of special sense organs namely: the skin, the few specialized tactile or taste cell groups, and the eyes. The skin seems highly receptive thruout its entire surface and is evidently the most important medium of communication with surrounding conditions. Only one cell in thickness, it serves as a most efficient conductor of stimuli of probably all general kinds. That it is extremely sensitive is apparent from the great number of contractions constantly taking place. On the ventral surface of the head there are several special groups or patches of more highly differentiated epidermal cells. These patches are each supplied with a special nerve branch and seem to be of value in selecting food and in ascertaining more exact details as to environment so that they may be primitive taste or rather olfactory organs. Each is composed of a cluster of several cells with rather heavy, rigid walls and denser cytoplasm. The whole head is generally in rather constant motion, parts are protruded or pushed around in all directions as tho investigating and locating any nearby source of food. It is with these sensory patches that such activity is carried on.

The most conspicuous development in the way of a sense organ is the eye. This is hardly more than a light-detecting organ, but is noteworthy because of its characteristic shape and color. The eyes lie one on each side of the middle line just dorsal to the brain ganglion beneath the epidermis. The carmine-red color of the pigmented portion makes them stand out sharply against the

clear head region. This color varies somewhat in different individuals but for the most part is heavy, dark, and very opaque. The outside surface of this dark part is exceedingly rough, covered with coarsely granular knobs. The shape, too, is irregular, very jagged, almost spiny, and often with flecks of pigment completely isolated from the rest. The position of the pigmented portion is quite constant. The pointed edge, which narrows out to a sharp, bent tip, always is placed toward the middle line, at right angles with it, and directly opposite the eye of the other side. The remainder of the pigment is arranged like a cone-shaped cap with the much serrated external edge clasping a very transparent lens-like cell. This lens is all but invisible so that the inner surface of the dark cap can be distinctly seen much lighter than the outside, and also much smoother. The crystalline part is a solid bean-like structure, not ever exactly alike in the two eyes, and varying enormously in both size and shape. The nerve supply comes directly from the ganglion on whose surface the eye rests. It can hardly be said that optic nerves exist, since there are only clusters of cells which send branches or divisions of protoplasm up into the pigmented layer. It seems hardly possible that such an irregularly shaped mass could be capable of being more than a light-detecting organ, but the nerve supply would seem to indicate some true seeing ability.

EXCRETORY SYSTEM

The excretory tubules are of the typical primitive type. They are protonephridia, rather large and well-developed, but exceedingly thin-walled and delicate, so that they are invisible except under very favorable conditions. The two long tubules have their beginnings somewhere posterior to the middle part of the body and the extent and size are variable, so that in some individuals the tip may be very near the tail. The tubule, not at all constant in its position, wanders forward thru the parenchyma, quite deep below the surface, until it reaches the neck-region, where it bends dorsally around the anterior end of the intestine. In the head it lies only a little way beneath the skin, being dorsal to the nerve and muscular systems. A little in front of the eyes and between them, the two tubules, one for each side, approach each other and then bend around ventrally, forming two loops. They then run back still in a ventral position till they reach the edge of the pharyngeal rosette, where they empty. Thruout their whole length these tiny canals are never taut, but are irregularly looped and folded so as to allow for a large amount of stretching without any strain to the delicate walls. The flame cells are difficult to find, owing to their diminutive size and the deeply embedded position of the tubule. In some instances, there are a number of these waving cells scattered along the length of the tubule, while often only one or two can be found. As a whole there is so little variation from the common type that a general description will apply directly to most details of this form.

REPRODUCTIVE SYSTEM

Only during a rather limited period in the year are the reproductive organs to be found. Then they stand out definite and heavy, easily recognizable among the other more transparent organs. The season of sexual maturity extends from about the first of November till the last of December, and during this time a single individual will produce several eggs. The animals are hermaphroditic but do not possess so complicated a series of organs as is generally to be found in this class. In brief, the reproductive organs consist of paired testes, a single ovary, with small vitelline glands and atrium seminalis which opens to the exterior by a short canal and pore situated on the ventral surface. The organs lie close together just posterior to the pharynx rosette, ventral to the intestine but to a greater or less degree displacing it. The group of parts thus formed makes a noticeably clearer region, oval in shape, much larger than the pharynx in extent and lying in the middle of the body. The two testes are situated on the right and left of this transparent part with the ovary between them and in all three instances the ducts open forward and ventrally into the atrium. The vitelline glands, having their connection with the ovarian duct, ramify for a short distance among the adjacent lobes of the intestine. During the development of the egg, which takes place in the atrium, the other organs become crowded to either side.

The organs, themselves, are characteristic and vary little from the general type. The testes are spherical with a rather large duct leading to the atrium. This duct is very broad at the point where it leaves the testis and narrows gradually toward the opening, which gives it a funnel-shaped appearance. The wall of both testis and duct bears a layer of muscular fibers lying parallel to each other. The wall is, however, of sufficient transparency to reveal the mass of sperm cells lying within. Thruout the whole reproductive period, the testes are tightly packed with sperm, all seemingly mature at least in size. The ovary varies a good deal in size at different times during the sexual period. It is made up of a mass of extremely large cells packed closely one above the other, crowded into narrow plates, from six to ten completely filling this organ. The shape is that of a pear but varies slightly toward the ovoidal. As the eggs become mature at the lower end, they round out and draw away from the mass little by little until they escape into the duct leading to the atrium. Fertilization probably takes place while the egg is still in the canal, which is very short, or at the time it reaches the atrium. The immature eggs are thin-walled with very large nuclei and finely granular protoplasm. By the time the last egg has become mature, the ovary is very much diminished in size and is ready almost to disappear. In the atrium, which by means of its heavy wall becomes the egg-capsule, the ovum goes thru the maturation stages, develops the yolk-cells, and gains the heavy wall so characteristic of it. The atrium lies on the median line and as the egg enlarges it becomes more and more conspicuous. By the time the ovum is ready for laying, it has a size nearly equal to that of the pharynx and has stretched the atrial wall to the limit, so

that the pressure is great and only a small amount of displacement will cause it to be extruded. The canal leading from the atrium to the external pore is short and held firmly in place by the surrounding tissues, but possesses a most elastic wall so that very quickly, when the pressure is sufficient, it enlarges many times to allow the passage of the egg. The pore itself has a very flexible wall, the epidermal cells flattening and lengthening to an almost unbelievable degree. At the close of the sexual period the organs are very much depleted and have shrunken, loosing also the definiteness and toughness of the walls so that the whole appearance is very different from that of the earlier period.

DEVELOPMENT

Individuals carrying eggs were first noticed about the middle of November and a few were found in every haul made during the next four weeks. One more appeared on the twelfth of January, but none later. In all cases these individuals were not as generally opaque as those not sexually mature, i.e., the intestine was not so clogged with food, and oil globules were present in only small numbers. The body was also much more slender, indicating either that the regular amount of food had not been taken or else that the strength was being used for the nourishment of the egg. Altho sensitive, they moved around less actively than the others and seemed almost to be lacking in vigor.

The egg, which develops singly, is carried in the atrium seminalis and is visible because of its opaqueness even to the naked eye. It appears as a thick whitish spot, a tiny spherical knob causing the surface of the body to bulge a little on both dorsal and ventral surfaces. Under low magnification it shows as a red-brown sphere, surrounded by a capsule made by the wall of the atrium. A little smaller than the pharynx rosette, this capsule generally lies just posterior to it and near the middle line of the body On account of the transparency of the body and the heaviness of the egg, it appears as conspicuous as the rosette itself. The egg capsule though retaining its relative position in the body parenchyma is very movable, recalling a balloon buffeted about in all directions but anchored to one spot by its tether, which latter is comparable to the short canal leading from the atrium down to the pore on the ventral side of the body. This pore is generally almost invisible, but, under some conditions, it is drawn up into a rather large papilla, just posterior to the pharynx. This drawing up is due to the contraction of muscles in its walls and in the surrounding integument.

As soon as they were discovered, animals carrying eggs were isolated in small watch glasses, where they were kept in about five cc. of water taken from the aquarium jar in which they were found. These jars had been filled with water containing a greater or less amount of algae, water plants, many crustacea, other rhabdocoels and an inch or more of mud and sticks at the bottom, in every way very much like the natural pond except in temperature, which was slightly variable being the room temperature. The temperature was, of course, very different from that of the water under the ice in the ponds, but

seemed to have little effect on the development other than perhaps to hasten it. This appeared true from the fact that in the hauls made every few days young individuals were constantly found in increasing numbers and of several sizes up from those smallest and evidently just hatched. When isolated, the individuals soon came to rest and easily accommodated themselves to the new surroundings. Since the watch glasses were so small, there was some change due to evaporation, but this was as slight as possible because they were constantly watched and the water replenished or completely changed. In order to prevent too much evaporation, they were kept covered with beakers. Part of the time the water was changed every three or four hours, and part of the time once in forty-eight hours. The water used to replenish was either clear, from the reservoir which supplied all the ponds, or else taken from the same aquarium as the individuals themselves and then carefully freed from all crustacea and other small forms.

At first the eggs were rolled around and moved by the force of the water from the pipette. They then either floated for a little time or slowly sank to the bottom. Two finally settled to the bottom and became fixed by a secretion of cement, so that their position remained absolutely unchanged thruout their incubation period. Others were rolled around more or less at different times. The parents were removed from the watch glasses just as soon as the egg was laid in order to prevent contamination of the water. Altho the individuals were isolated at different times during the day, in all cases the eggs were laid sometime late in the afternoon, the earliest at 2:30, the others about 5:00. It appeared that when the egg was ready or nearly ready for laying, it required only a slight disturbance of any sort to bring this about. For example, in the case of egg number four, which was laid at 2:30 P.M., as the stream of fresh water entered the watch glass from the pipette, the animal somewhat aroused, contracted only slightly, but moved rather quickly about the dish for a moment, and just that small amount of extra stimulation was enough to cause the egg to be extruded. In all the other cases where the egg was laid several hours later in the day, the parent was quiet, more or less drawn up, clinging to the side of the glass or resting on the bottom.

The eggs vary slightly in shape, size, and color, showing perhaps the individual character of the mother. Never quite spherical, they can hardly be said to be ovoidal, the measurements averaging 145 by 140μ. The outline of the egg is thus a very round-ovoidal sphere. Sometimes, however, one end is more pointed than the other, giving almost an ellipsoidal appearance. That the shape is far from perfect was evident when the egg was rolled over and there came into view variations in the outline and in the amount of bulging in the different parts of the surface. The color is a rather clear deep yellow, verging a little on the red and brown, and is lodged entirely in the shell. This was demonstrated when the egg was broken and the white yolk was lost or when the embryo escaped after hatching, leaving the empty yellow shell. To

the naked eye, the egg was a reddish-brown speck just barely visible, and appearing quite dark. Under some magnification and with reflected light, the yellow was much stronger altho the influence of the white internal portion of the egg was more noticeable. The shell though rather thick and heavy is quite transparent and clearly shows the yolk granules in the younger stages and the details of embryonic structure in the later.

Figure 10 shows the egg as it appears during the first few hours before segmentation has begun. The yolk granules give a cellular appearance and near the center can be seen the nucleus, rather large and with a heavy wall. The granules vary in size, some being not more than one-quarter as large as others. They are slightly milky, somewhat transparent, almost a pure white, irregular in shape, angular, due partly to pressure, and closely packed. When the egg is broken, the granules escape into the water in a mass, the individuals adhering closely, and holding their shape even when separated. Very little change could be noticed during the first six hours, but soon after that the even appearance was lost, as at different points there seemed to be a breaking or drawing apart of the granules, showing lighter streaks. During the first twelve hours, the first and second cleavage stages were finished. The divisions were not distinct, showing very clearly only at the edge where a notch marked the rounding of the cells.

By the end of the first thirty-six hour period, the cell divisions were much more distinct, the cells had attained a spherical shape and had arranged themselves definitely. The macromeres could be distinguished drawn to one side of the egg while the four micromeres appeared toward the center and opposite side. At different times the nuclei of all the cells were visible as small, round shadows. The spaces left by the formation and shaping of the cells became more transparent so that the outlines were distinct and the whole aspect of the egg was changed, i.e., the cells were adhering to each other only slightly, but still in one integral mass, and were floating in the surrounding fluid. The macromeres were very large, about one-sixth the size of the egg and were arranged as a hollow plate, while the micromeres, somewhat smaller, lay curved inside. By turning the egg slightly different views of the various cells could be obtained, and their relations made out.

During the next few hours, the division stages continued. In many cells, the new walls could still be distinguished but the mass soon became so solid and opaque that it was impossible to follow the cell lineage with any degree of accuracy. The two poles of the egg were marked by the difference in cells which at the micromere or animal pole increased in numbers, and soon filling it began to push down as a cap over the large macromeres. At the beginning of the third day the cap of small, compact cells had extended more than half way over the egg, giving a typical gastrula stage. This was very conspicuous and characteristic, as the cells at the animal pole were dark and heavy, while the free portion at the opposite end was clear and transparent. During the third and fourth days the mass of cells in some places grew to extend all the way around to the ventral side.

The changes which take place during the fourth, fifth, and sixth days are those striking in their effect upon the appearance of the embryo. During the fourth day the appearance is that of a mass of cells surrounded by a thick wall. It is at this period that the masses of the various organs differentiate themselves and instead of a mass of cells the several tissues and organs begin to be apparent. The first noticeable change is in the wall of the embryo which develops into a clear, very thick layer so closely attached to the inner surface of the shell that it seems to be merely a lining membrane. That this is really the integument or epidermal layer of the young worm becomes evident when, thru the lengthening and expanding process, this wall is folded in, away from the shell. Both outer and inner boundaries of the epidermis are sharply defined, so that the latter is a conspicuous portion of the embryo. The extreme thickness of this layer may be explained by the cramped and contracted position. During this same period the muscular system begins its growth as many strands of cells attached to the firm inner wall of the integument. Thruout the following days there is an increasingly greater amount of contraction and movement of the whole surface of the embryo. It is constantly being spasmodically drawn in at one point or another for a minute and then slowly released, as tho the different fibers were each receiving their quota of exercise.

About this same time, also, the start of the intestine made its appearance as a mass of cells nearly in the center of the egg, the connection with the mouth not taking place until later. It was merely a plate-like layer of cells at first, without any of the lobular ramifications of the adult organ. Little by little, out thru the parenchyma, small strands of cells became differentiated and enlarged as branches of the main portion of the digestive tract.

Both anterior and posterior ends began to lengthen so that the spherical condition was gradually lost and the much folded, much crowded elongate worm was distinguishable. The two extremities were clear and very conspicuously different from the heavy, dark middle portion. In the anterior end the mass of cells which forms the brain ganglion began to take shape and a little later the eyes could be seen. The two loops of the excretory tubules as well as the strands of rhabdites were visible. There was constantly a very slow rotating of the whole worm in the shell. It took sometimes from one and one-half to two hours for the whole embryo to turn completely over and it was rather difficult to distinguish the different parts, as the embryo was much twisted. At other times, the movement was much more rapid for a minute or two, and then the embryo would remain quiet for some time.

By the morning of the seventh day the worm was slowly twisting and turning almost constantly, often making a complete rotation in a few seconds. About this time at points where the integument was drawn away from the shell, in the space thus left, long and well-developed cilia could be seen vibrating rapidly in their close quarters. As soon as the wall returned to its position against the shell, the cilia flattened down and were again invisible, altho their influence must have been felt as aiding in the movement of the body as

a whole within the shell. It was clear, however, that the development of the cilia was parallel with the increase in the rapidity of motion, altho the muscular system also had something to do with this motion The intestinal tract was beginning to have a more definite boundary and to extend both forward and back, and to a slight extent around toward the ventral side. During the latter part of the seventh day the eyes began to be distinguishable as very irregular brownish-red masses. They were almost crescent-shaped with the center somewhat pointed and jagged. They lacked, however, the extreme roughness of the adult form.

By this time, also, the several folds of the integument were lost and the worm had straightened out, doubled only once upon itself with one long fold cutting thru the middle of the egg, so that the anterior and posterior ends lay against each other at one side with the dark mass of the digestive tract around on the other side. Thus, the whole ventral surface was turned toward the center.

During the eighth day one side of the egg showed a fine, dark line running around a portion about the outer surface of the egg. This line became more and more distinct and appeared like a crack in the shell. Its significance was explained later. The rhabdites at this time were still very small and difficult to distinguish on account of their transparency, but were fast taking the shape of the adult condition. They were arranged a few in each cell, but the number for a cell was smaller than in the adult. The mouth and pharynx rosette were also nearly complete. The two heavy, perfectly circular muscle strands and the intervening rosette muscles were complete. The reproductive organs were not developed, the atrial pore not broken thru, the papilla showing not at all.

The embryo was, by this time, very often rotating within the shell and was almost constantly contracting one portion or another. The intestine now extended well up toward the head and back almost to the end of the body where it was broader and thicker. In a lateral view it could be seen extending ventrally to the rosette and the ventral wall. Several rather small oil globules appeared in the wall, giving the characteristic orange color. These, however, were very few in comparison with the number which showed even immediately after birth. The embryo had, by this time, evidently begun its metabolic processes and was an almost perfect individual.

During the first few hours of the ninth day the ring in the shell became very conspicuous as a point of cleavage and gradually, bit by bit, the cap-like portion pulled away from the rest, lessening the pressure within the shell and causing a cessation in the movement for the time being. Later, the embryo began struggling again, the force finally splitting the cap more than half way around and allowing it to spring up so as to permit the little worm to squeeze out thru the opening, leaving the empty shell intact. The cap fell back almost into place The newly hatched worm very closely resembled the adult except in size. It moved about very slowly at first, then more rapidly, and in a short

time was taking food in the same manner as adults. The color was that of the adult except that it was very much ligher. The size was 0.75 by 0.6 mm. to 0.86 by 0.65 mm. The animal was a little more slender than the adult.

LIFE HABITS

The surroundings and immediate environment of these forms are much the same as those for other rhabdocoel species. *Strongylostoma rosaceum* lives in ponds containing a rather large amount of green algae and perhaps some few other water plants, with usually a muddy bottom more or less deeply covered with leaves, sticks, and organic debris. The other animal forms common in the ponds are such as will be found in very many other representative puddles. About twelve species of Cladocera, fifty rotifers, about a hundred protozoa, ten or twelve aquatic oligochaetes, besides very many insect larvae also inhabit these ponds.

Several environmental factors are of some detailed significance, perhaps the most vital of which is the water condition. The oxygen content seems to have little direct relation to the life processes, as the animal carries on its existence with seemingly equal ease in the clearest, freshest water, containing a high percentage of oxygen or in water heavily laden with carbon dioxide. The pond water altho constantly kept in motion by a steady stream running thru it, was often, especially near the bottom, very thick and muddy. Sometimes thoroughly clogged with algal masses so that many parts were dark, it also supported an extraordinarily large population of animal species. Owing to a lack of balance a number of times in the aquarium jars, the water became very stale so that there was a great amount of bacterial growth and much of the algae died. Such conditions were, of course, fatal to a great deal of the animal life and in time would do away with those of the flatworm type also. These, however, seemed to withstand such adverse conditions longer than most of the others. The water temperature varied within very wide limits without causing any great difference in life processes except, perhaps, in the case of the reproductive organs. The summer temperature is high and when standing in a sunny window, the aquarium jars were often warm. Here the animals thrived, being more active in the warmer water. On the other hand, the reproductive season comes during the early winter months and that it is in the coldest months that the young generation starts its life independently, is a fact probably to be correlated with the low temperature. Thus the vegetative activity seems greater in warm conditions while the reproductive organs function alone during the winter. However, the life-cycle seems to be completed very soon after the eggs are laid, the individuals not existing thru all seasons. This may be due solely to the depletion of organic strength or, as seems possible, to the fact that the severest and prolonged cold comes at a time when the animals are weakened and unable to withstand such rigorous changes. The reaction to light is positive but neither precise nor immediate. When placed in watch glasses of water, lighted from one side, the individuals

will always find their way to the lighted part after some time has elapsed. This was also true in large aquaria, but the response was not as constant, due to influence of other factors.

The feeding habits seem to be the result of the surrounding conditions. Altho active and much of the time living in open water, these animals do not attack living forms. Live, hard-shelled Cladocera and rotifers would be difficult for such soft, unarmed forms to manage, and even the smallest protozoa appear to be safe from their depredations. Repeatedly, upon encountering a most defenseless protozoan, the rhabdocoel will glide over it and leave it unharmed. However, the whole attitude is changed when the prey is dead. Very often the dead shells of small crustacea, some of them many times the size of the rhabdocoels, are found entirely covered by an active hungry mass, eagerly devouring every bit of edible portion. It is quite impossible to dislodge even a single individual without crushing or injuring it, so tenacious is their hold. Figure 3 shows an empty shell of a Cyclops being cleaned out thoroly by a few individuals. As they worked, it was possible to see how industrious and intense was the habit and manner of finding every particle of edible material. They remained within the shell for more than an hour, constantly at work, until it was completely emptied of all soft material and ready to fall apart. The animals themselves were by that time fully gorged and showed the digestive cavity dark and large, obscuring even the pharynx rosette. Ostracod shells seem easy of access and are very often cleaned out in this same manner. Dead protozoa, also other soft bits of animal debris, are eagerly attacked and devoured and it is probably in search of such particles, which may be caught in the masses of algae or have reached the upper layer of soft bottom mud, that the individuals are seen in large numbers finding their way hither and thither in the deeper portions. This may also explain the fact that water, dark with masses of organic debris, forms good feeding ground, so that instead of being an unendurable condition, it is one in which there is possible greater vegetative activity. The rôle of scavenger is thus played by these small forms and their place in the balance of animal life must be an important one. Hardly to be considered as enemies of even a single individual, they are merely one of the types without which other more aggressive species could not exist.

It seems probably that so unarmed and defenseless a creature as this must have a number of enemies, but evidently they are almost negligible. From an enemy like the fish, which takes in large amounts of water, the tiny rhabdocoel has no escape and no method of defense, and numbers must thus become the food of large forms. Others will stray into the jaws of some animal along with the water, e.g., the crayfish, but the smaller crustacea seem to make little headway in an attempt to kill and eat these dainty morsels. Ostracods have a habit of attacking a resting individual and by means of strong appendages tearing a hole in the skin. It takes a good deal of persistence to

accomplish this, however, as the rhabdocoel will either draw up into a compact ball hard to take hold of or will swim away, scraping off its tormentor in some mass of algae. Many, of course, must meet their death caught in some maze of filament or mass of loose mud, but in open water they seem to be safe and able to swim quickly away from any danger. It may be, of course, that the taste is not delightful to some forms or the presence of dermal rhabdites may make them unfit for food. In some way they seem to be able to live a life singularly free from attack and they mingle in the most courageous manner with many species of larger forms, tho for the most part lurking in some secluded part of the deeper water and coming out to the light only occasionally.

They move very gracefully with but little muscular contraction. The coat of cilia serves as an efficient organ of locomotion and the result is a very even gliding, lacking entirely the twisting and turning so characteristic of other types. In pushing thru small openings or entanglements, there is more or less muscular contraction but otherwise the cilia are able to propel the body unaided.

In case of slight injury there must be some amount of regeneration possible, but there is little evidence of this. Among thousands of individuals examined, none were found in the process of healing wounds or regenerating lost parts. This fact is conspicuous in comparison with other species where scars and wounds of one sort or another are common. With the above may be correlated the fact that no asexual budding has been discovered. It would appear, also, that a form of such complexity does not possess the power of unlimited regeneration but a condition of entire lack seems improbable. Further study will doubtless reveal some possibility along this line.

Typhloplana viridata (Abildgaard) 1789

Figures 22, 27, 30, and 31

This is another species taken frequently during April and occasionally in the summer and fall. My individuals, although very evidently to be identified with the European form, vary somewhat from that, and also from those specimens hitherto found in this country.

The animals seem to come entirely from bottom water or from masses of algae living close to the bottom. The size and shape variations are perhaps the most interesting. The exact length is exceedingly constant. More than three-fourths of the individuals measure 0.5 mm. There are differences, however, in the plumpness so that the animals do not appear alike. The other one-fourth of the individuals seem in comparison, very long and slender, for, while they measure only 100μ more in length, the relative width is much less. The shape is quite different from other forms. The slope toward the tail is much more gradual altho the tip itself is not sharp; that is, the posterior region is not blunt and stubby, but more slender than is usual. The middle part of the body is round and not so cylindrical; then, too, it slopes into a slightly narrower neck-like portion which again rounds out into the head. This

head, except for shape, can hardly be differentiated from the tail end, as it does not possess eyes or specialized sense organs of any sort. It is quite round and nearly as broad as the widest part of the body, tapering not at all. On the whole the shape of these specimens is more like that found in some of the related genera than it is like this species. The anterior end is much more contractile than the rest of the body, there being almost no contraction possible back of the middle line. The amount of contraction, however, is very much less than in most nearly related species, and neither is there the twisting and turning which is characteristic of other types. That is, the body seems stiff and solid.

Even to the naked eye the color varies. It depends upon the amount of green present and is sometimes deep and brilliant, at other times pale and often almost gray. This gray is the real color of the parenchyma, due to absence of the pure green coloring matter. When there are a number of winter eggs, large and nearly mature, they alter the general appearance, giving a dull brown tinge which sometimes may be quite dark.

The integument is very clear, showing not at all the cellular divisions so plainly to be seen in some forms. It thus seems almost homogeneous. The cilia are not clearly noticeable, as they are very fine and not differentiated. The rhabdites are very small and lie in the parenchyma just beneath the epithelium. They are not arranged in definite tracts but are scattered evenly thruout the body. The thickness of the integument is somewhat surprising, as for such a small form it would hardly seem proportionate for the one layer of outside covering to reach a thickness equal to one-tenth the body diameter.

The parenchyma is unique in every respect. The only cells which are conspicuous are those which contain the bright green color bodies. These bodies are spherical and all of about the same size. They are arranged in a nearly solid mass in the cell wall, which is in every instance so filled that the surface shows the outpushings of the solid bodies within. This makes the surface slightly rough. The wall, however, is fine and delicate, partially elastic so that the boundaries of the green bodies are visible. Most of the cells contain from six to ten bodies but an expecially large one may have as many as eighteen or twenty-five. These zoochlorellae or color-bearing cells are not at all regular in their placing, being scattered a few here, a few there, thruout the whole body. There were never, however, very many in the part anterior to the pharynx, a fact which makes the head much lighter in appearance. Other parenchyma cells are of the common transparent structure and are hardly visible unless the zoochlorellae are so nearly absent that the remaining cells are not obscured. The thinner material which makes up a part of the colored mass is more sharply differentiated than in other types. Its very homogeneous fluid nature is evident. This fluid is a very smooth light green, but whether the color is merely a reflection from the zoochlorellae or is an intrinsic quality developed as a result of their action is hard to ascertain.

In most of the specimens taken during the spring a number of eggs were present. These varied in number from one to ten, and it is probable since it was near the last of the winter season that in those individuals carrying one egg, this was the last, the others having been laid, rather than that it was the first with others to develop later on. The one or two eggs always lay in about the middle of the body, and where there were more, they crowded forward toward the head, sometimes almost completely filling the whole anterior half or even two-thirds. They were in two rows except in a few instances where one, the oldest, occupied a position ventral to the others and nearer the sexual pore. Since these were winter eggs, it was not surprising to find them with very thick shells. These shells were dark brown and about one-ninth the diameter of the egg in thickness. For the size of the animal these were very large, measuring 80μ to 120μ across. The yolk cells showed thru very distinctly and were all of the same size. They were large and few in number, giving a very different appearance than in the case of those where the yolk mass is finely granular. With a strong light the nucleus was visible as a large clear spot. Of the other reproductive organs, the cirrus could be made out large and almost transparent in the parenchyma. It was nearly as large as the pharynx and clearly showed the concentric layers of cells in the wall. The sexual pore was guarded by a broad band of circular muscles. The testes appeared large and solid.

From the several descriptions given by different authors and in the above details, it would appear that this species undergoes a greater amount of variation than is possible in many forms.

Mesostoma ehrenbergii (Focke) 1836

In Europe, Asia, Greenland, and Australia, as many as fifteen species belonging to the genus Mesostoma occur in great numbers thruout many very widely separated regions. The general appearance of unhampered development, i.e., large size, bright color, plumpness, number of eggs, etc., seems to indicate that the varied conditions under which they live are perfect, in most respects at least. A few species are confined to a limited area, but most are to be found in both northern and southern lakes or streams. In the United States the situation appears to be different. Hitherto the presence of a Mesostoma has been reported in only four localities, and in two of these merely a few scattering individuals were seen. In each instance *Mesostoma ehrenbergii* was the form identified. That this species and also others of the genus may be present in many places in America seems probable. The hardiness and adaptability so evidenced in the rest of the world would indicate that these forms are to be looked for here also.

Among the twenty rhabdocoels which have appeared in Mississippi valley ponds, it is thus to be expected that some Mesostoma might be present. So far three species have been studied. Two of these, *Mesostoma angulare* and *Mesostoma simplex* are new and different from the old world types. Another,

Mesostoma ehrenbergii, mentioned above, is especially noteworthy. For, although recorded only twice before now, and then each time as only a few individuals, it was the first of the whole group to be discovered in this central region. Twenty years ago Woodworth found it in the Illinois river at Havana. Now, in one of my collections from the same place a single specimen was obtained. This crawled out from a tangle of waterweed which was brought in from overflow water. Persistent efforts to find other individuals failed.

The general characters were very distinct so that the identification was easy. Some variations, however, are worthy of note. The size was 7mm. The shape of the body was a regular long rectangle. Both ends instead of being more or less pointed, were truncate. This was less noticeable when the animal was in motion but even then the square projecting corners were evident. These portions of the head seemed sensitive and constantly investigated the immediate surroundings. They call to mind the auricular appendages of Planaria. Together with the smooth contour the very flat leaflike condition was conspicuous. Even allowing for the lack of thickness due to the small undeveloped eggs, my specimen was very much flatter than the European forms. And compared with them the whole body shape was especially characteristic, more regular, smoother and depressed to the thinness of paper. The extreme transparency added to the weird effect. Against this clear background the small eyes showed black and distinct. They were very near together, regular in shape, lying on the dorsal surface of the brain ganglia. In front of the brain the rows of rhabdites were large and well defined so that the anterior part of the head appeared gray. The reproductive organs showed very clearly their outlines and the row of summer eggs lying regularly arranged in the uterus. Almost in the middle of the body, the pharynx lay with its wall heavier and more noticeable than in foreign individuals.

It is impossible to draw any general conclusions from a single worm but these points of variation may lead to a better understanding of the adaptability which has been so evident in old world specimens.

Mesostoma angulare nov. spec.

Figures 29, 41, 45, and 55

Twenty specimens of this unique rhabdocoel came in the hauls from a pond near Urbana. Later the same form was found in the Illinois river at Havana. It is interesting to note that here is a form resembling in some respects the European types and yet in many ways distinctly different. These worms are essentially bottom lovers, tho they very quickly creep into and thru any heavy mass of filamentous algae. The length was always between three and five millimeters, the width not more than one-fifth the length, while the greatest depth was only a little less than the width. Both these measurements, however, differed greatly in the different specimens and in the same specimen at different times. The whole shape was slender, cylindrical in a general way. The head end showed the characteristic conical, bluntly pointed portion with

the rhabdite tracts very conspicuous. It was flat and moved constantly in all directions. The tail was not pointed sharply but tapered to a short, blunt tip. Some of the specimens were much inflated with young worms, but this inflation was almost entirely effected on the upper surface alone. At a point just posterior to the eyes the body wall very sharply rounded upward, making the head only a flat projection on the ventral anterior border of the whole mass. The posterior end narrowed more gradually. In any collection a good many young individuals appeared. These were always more regular in outline, the head and tail ends tapering not at all and the width being nearly the same thruout the body.

Another rather distinctive detail was conspicuous in specimens not swollen with young. This was a definite fold or angle about midway between dorsal and ventral surfaces and running from near the anterior end far back, almost to the tail. This fold is marked by thickness of the epithelial cells and by two stripes, one dark, one light. It somewhat resembles the middorsal ridge of *Mesostoma tetragonum*. However, in this latter species the form is exceedingly flat and broad, causing the ridge to appear as a mere projecting fold on the upper body surface. In my specimens, on the other hand, the cylindrical shape carries the ridges outward making them sharply angled corners, and giving a very characteristic appearance to the body as a whole. In individuals distended with young worms the folds are entirely obliterated. The line of demarcation between the dorsal and ventral surfaces is also definitely developed as a lighter, heavier streak. Since the ventral surface is flat, this line is never to be seen unless the animal lies partially turned on one side. This ventral line and the lateral fold are very much alike in appearance and structure.

The color varies from a delicate to a dark brown and is lodged in the parenchyma. For this reason the anterior head region in which there is little room for middle cells is entirely clear. The color is not the same over all other parts of the body but is concentrated in a wide dark strip down the middle of the dorsal surface. Then, also, the folds and angles along the edge are banked by a heavier band. Young individuals show very pale yellow and those just born are entirely without color.

The rhabdites occur in the parenchyma in close relationship with the color cells and are sharply defined and clear. They lie in groups of six or ten or are promiscuously scattered. The head also shows heavy tracts. In shape they are straight rods with rounded ends and without any variation in diameter. Under a lens the rhabdites give the parenchyma a checkered, rough appearance. Two details of digestive tract structure which stand out clearly are, one, the narrowness of the intestine, the other the shape of the pharynx. The intestine instead of spreading out through the parenchyma, is rodlike and consequently more compact and of greater depth than that of most species. It extends only as far forward as the eyes, a possible reason being the lack of space in the head. The pharynx rosette is here almost spherical as differing from the flat funnel found in other related forms. The inner dorsal surface

cuts off only a flat segment, and the margin thus left seems drawn in, partially rounding and obliterating the opening to the intestine. The mouth is small, appearing as a hole in the ventral wall.

The most striking detail of the whole body structure is, perhaps, the complex reproductive system and viviparous habit. The yolk glands lie next to the intestine and are opaque to such an extent as to be easily distinguishable from the other organs. The ovaries and testes are inconspicuous except during a short period of especial activity. A number of specimens each bearing several developing worms, were examined. In one of these, twelve embryos could be seen, seven in the right and five in the left uterus. They were closely packed and most were somewhat curled up, the anterior end sharply bent on the posterior. The movement was mainly a constant stirring, the several worms gliding over each other more or less, and to some extent changing their position in the body. The mother was finally killed, cocaine being used to produce anesthesia. By this method, the regions of greatest contraction were made out. The head and the region posterior to the pharynx are drawn toward the anterior middle part which very greatly increased in diameter, making a heavy knob-like portion. These contractions drove all the embryos to this region where they were tightly massed. Another specimen showed seventeen embroyos on the right side and twelve on the left. These were large, one-fifth the total length of the body of the parent, but were not so confined as the younger specimens. The wall of the uterus is heavy and not elastic, but so enlarged as to give ample space within. All the young worms were active and incessantly hurrying from one end to the other, crawling over each other in the most promiscuous way. This enlargement of the uterus pushed toward the center both the intestine and what little remained of the yolk glands. The testes had almost completely disappeared so that the main portion of the body on each side was occupied by the large transparent uteri. These, however, were extended only as far forward as the head region. The extra space needed was gained by a dorsal swelling, the central upper surface being extraordinarly extended, making the shape of the animal most grotesque. The two uteri connected with each other across the middle line by uterine ducts but there never seemed to be any intermingling of the individuals from the two sides. This was evidently due to the fact that the duct was too small to admit of the passage of large worms. By the time the embryos are ready for birth the duct is stretched but even then the tendency is to pass to the exterior rather than across the body, since in the outward direction the resistance is less. The young worms in this specimen and in the one mentioned above showed clearly two of the later stages of growth. In the first, the embryos were not long in proportion to width, the head was not at all marked off from the body regions, and the intestine was nearly clear. In the second example, the embryos were much more elongate, the head tapered off slightly and the intestinal wall was visible as a light gray with many very regular globular cells. The eyes in both were prominent. In the older worms the pharynx was also fully developed and

in fact more conspicuous than in the adult, because of the transparency of the parenchyma and also because it was relatively very much larger. The tracts of rhabdites had also become heavy enough to be visible and most of the body structure was perfect. When, by accident, the body wall of the parent was broken, all the embryos pushed out and swam away, seemingly perfectly at home. In the collections together with the adults a larger number of small individuals always appeared. In size these outreached the unborn embryos only a very little. Thus it seems that the young are retained in the body of the mother until a very late stage in their development.

With the exception of a few scattered individuals of *Mesostoma ehrenbergii*, this is the largest rhabdocoel known in the United States. Examined superfically it might be a small planarian. However, the angled cylindrical body, the depressed head, and the viviparous habit mark it as a typical and also specialized Mesostoma.

Mesostoma simplex nov. spec.

Figures 32 to 38, 40, and 42

A number of specimens of this form appeared in a pond together with *Mesostoma angulare* and others of the same family. In many respects they closely resemble the more common species. That is, the general shape, the pharynx rosette, the slender body, the black eyes and the anterior tracts of rhabdites, differ very little from those of other species. In certain details however, they vary to a surprising degree, being decidedly different from associated types.

Several points of general appearance are notable. The size, altho not at all constant, is not over 1.5 mm. long by 0.45 broad and 0.3 in depth. This is much below the average for other Mesostomas. In shape, the difference between this and other species is more pronounced. The head end is rounded, tapering only a very little, and not at all constricted or differentiated from the body region. The diameter is about the same at all points except, of course, there is some little narrowing toward the tail. The head end is contractile and as the animal moves, it is turned from side to side and stretched in various directions. This causes more or less change in general shape, the tendency toward a pointing of the anterior tip showing most conspicuously. The ridge dividing dorsal from ventral surface is well-developed around the head and this often comes into view as the animal reaches up and out. The color is a light yellowish-brown and is usually lodged in the parenchyma. It is very even all over the body, which is quite the opposite from the condition in *Mesostoma angulare*. The anterior end, even, is not the least different in tinge from the rest. The integument is thick and clearly defined. It is transparent and of nearly equal thickness all over except at the lateral ridge and in some special anterior portions which seem to be more sensitive. The cilia are not heavy and are evenly distributed over the whole surface. The rhabdites are scattered in a layer throughout the body just beneath the epithelium. Then, also,

there are several prominent tracts arranged in a narrow fan in the middle part of the head. These lie dorsal to the brain, running back between the eyes, but only far forward are they heavy enough to be noticeable. They are not so conspicuous as those of *Mesostoma angulare*, where they are sharp against the clear background. The parenchyma of this new *Mesostoma simplex* is especially well-developed, taking up most of the space in the body. The cells are close together and there appears to be less fluid than in some forms. The contained matter makes only the central portion darker and does not at all obscure the pharynx which stands out dark and heavy. Its size is comparatively large and the rosette cells are rather long. The species has not been taken when in the reproductive stage. The above outline summarizes the notable characters.

FAMILY GYRATRICIDAE

The Gyratricidae, the smallest family among the Calyptorhynchia, or proboscis-bearing rhabdocoels, was named by von Graff in 1905 to contain one genus. This genus had been described by Ehrenberg as early as 1831 under the name Gyratrix. Because of one significant character, namely the presence of two sexual pores instead of one, it was distinct from other nearly related forms, standing entirely alone. Such a detail of structure made the separation of this from other groups, the only logical division, and also elevated the genus to the importance of a family. Von Graff's classification was a very natural one. Thus far only three species have been named, one of which, however, shows three varieties.

In Europe the distribution is wide spread, the same forms being plentiful in the freshwater lakes and along the salt shores of the sea, in the warm Mediterranean and along the icy coast of Helgoland. In America *Gyratrix hermaphroditus* and two of its varieties have been reported as occurring in fresh and brackish water at Woods Hole, Massachusetts, and at two places in New York state.

Gyratrix hermaphroditus Ehrenberg 1831

My first specimens of this family were found at Havana, Illinois, in July. They appeared rather frequently in nearly all of the collections made from the many sloughs and overflow waters along the Illinois river. When buckets of material were brought into the laboratory, almost as soon as the water was quiet, these delicate rhabdocoels could be seen swimming out from the felt-work of algae. Under such conditions generally they were the first species to venture from their hiding places. This was probably due to the fact that the natural habitat is not the deep recesses of plant entanglements, but the outskirts of the mass where the water is freer. This same free habit, when circumstances were favorable, could be watched in native surroundings. If, for example, a place was found where a large mass of Cladophora was floating under the shadow of some tree, and if care was taken not to disturb or ripple the surface, then, against the dark background of the algae, the tiny whitish

forms could be easily seen gliding around in the more open places. With the aid of a small magnifying glass much of their movement could be watched.

In general the body motions are very regular, much more so than in types like Mesostoma, which crawl about in the depths of algal labyrinths. As von Graff says, Gyratrix is extremely contractile but this power is manifest only in a longitudinal direction. That is, the head and tail regions may be so drawn together that the shape is nearly that of a sphere; but, on the other hand, the head is rarely twisted or turned to one side, and the animal never bends upon itself, but always maintains a straight position. It glides evenly and often rather rapidly in nearly a direct course never pushing, here and there, or hunting in one place and then another. The locomotion is more by means of cilia than by muscular contraction of the body wall. The cilia are very small and practically the same size. The food seems to be gotten, 'hit or miss,' rather than hunted out. The individuals sail aimlessly about till they happen upon food. When coming in contact with something hard or unfavorable the animal quickly contracts and then changes its course—never investigating or crawling about as some species do.

The length of European species is given as 2mm. Few of my specimens measured over 1mm. This however, may have been due to conditions of that special locality, or to the season of the year. The body is slender, the greatest width being only one-fourth the length, and slightly flattened on the ventral surface. The shape is somewhat significant. The widest region is far posterior, generally at a point between the two sexual pores. The posterior end is bluntly rounded while the anterior part narrows evenly and gradually to the proboscis tip. There is no pigment so that by transmitted light the body is very clear, even the thickest part being almost transparent. To the naked eye the color, as seen against a dark background, is a thin greenish white. This is noticeable since most forms are quite dense or opaque in such a situation.

This transparency is due probably to the lack of a large amount of parenchyma. The slender body is nearly filled with the few body organs and since there is little plumpness, there is little room for large interstitial cells. There is also little evidence of many muscle fibres. The body wall cannot be drawn in at any point as in other species. The few muscles needed are developed in connection with the reproductive vesicles and the anterior body tip. Then another thing tends to increase the transparency; there are no rhabdites, so that the epithelium seems very thin. Also the intestinal part of the digestive system has a delicate wall, allowing whatever food material is within, to be plainly seen. Most of the specimens however, showed only small amounts of pale greenish material in the intestinal tract. They are evidently not heavy eaters. The rosette of the pharynx thus shows quite plainly, a little anterior to the middle. It is made up of rather slender thin-walled cells, so that the divisions are not very easily made out. The outside boundary, also, is not thick, since there are no extra cells.

Against this light background the proboscis is conspicuous both because of its structure and because of its constant motion. The proboscis itself is a transparent narrow barrel-shaped organ criss-crossed by exceedingly fine shimmering lines. The anterior cone-shaped piece is different, being clearer and lacking the lines. The whole lies in a sac-like sheath which opens by a narrow but distensible canal toward the front. The proboscis is at frequent intervals violently jerked forward and back, or sideways, in its sheath. Its function is a little obscure, for though evidently sensory, it is deeply buried and not protrusible.

Of the whole body the reproductive organs are the most conspicuous parts. The difference between right and left sides is apparent even to the naked eye. The large vitelline gland on the right gives that side a thicker whiteness. The small ovary together with the egg capsule are both distinct enough to be easily made out lying in the center. It was almost impossible to see the testis in any specimen since the color was nearly that of the underlying intestine. The complicated copulatory apparatus in the extreme posterior region is the most noticeable detail of all. The stiletto is chitinous, very large and heavy. Together with its sheath it makes a heavy rod reaching up thru fully one-fourth the body length. It lies a little diagonal to the middle line, extending from a ventral posterior point up thru to the dorsal side. The relation of this one strong stiff part to the neighboring soft tissue is very easily seen as the animal turns over or contracts.

In the same surroundings and often in the same collection both the type species *Gyratrix hermaphroditus*, and the variety, *Gyratrix hermaphroditus hermaphroditus*, were found. The difference between these two forms was quite evident since in the specimens of the variety, the point of the stiletto-sheath was very sharply recurved. The numbers were about one of the variety to ten of the typical individuals. It is interesting to note that the forms were living side by side.

About the first of August a number of specimens of *Gyratrix hermaphroditus* were found in Cedar Lake. This is one of the smallest lakes of the group in northern Illinois which forms the source of the Illinois river. It is connected with other lakes only by a very small stream which is during part of the summer entirely dry. The general conditions here, however, are practically the same as in the Havana locality, except that in many places the bottom is sandy and the water clear. Since most of the aquatic fauna is the same in both places, this similarity among the rhabdocoel species is to be expected.

CONCLUSIONS AND SUMMARY

Of the sixteen families which make up the Rhabdocoela, representatives of five have been found in the United States. Up to the present time, about eighty species have been identified from the eastern states but only sixteen from the central region. To this list of sixteen can be added, as a result of this study, eight new species and new localities for fifteen known forms. From the collections just made it appears that a great many forms found along the seacoast and in the border regions are also present far inland. The biologic conditions in the lakes and streams of the Mississippi Valley are not widely different from those of the ponds and rivers of the eastern slope and evidently the same species are to be looked for in both regions. When, however, such a form as *Microstoma sensitivum*, which is present in the brackish water of the open shore in Massachusetts, appears again in the small ponds of New York and then is found in isolated puddles in Illinois, some note must be taken of its power of adaptability, and some consideration must be given to the fact that a species so fragile and delicate may flourish in situations far removed from each other and of such different conditions. Other examples of a like nature are many, and it seems not too presumptuous to conclude that while few North American species are identical with those of Europe, the forms within the United States not separated by more than a few thousand miles will prove to be identical.

Another point of importance in connection with the distribution is the amount of variation found in individuals of the same species living under different habitat conditions. This was noted long ago, in the difference in average size among specimens of *Mesostoma ehrenbergii* from Europe and from the United States and in the differences in both size and shape of *Rhynchomesostoma rostratum* from the two countries. Then, too, many minor variations are exhibited among individuals evidently of the same species. This possibility of change is apparent in nearly every one of the old species found for the first time in the central localities. These variations are not of either histological or of gross anatomical structure, but are rather in the relative and comparative development of the several body organs. For example, the eyes may be larger or smaller or different in position in specimens from one pond than in those from another. *Prorhynchus applanatus* and *Typhloplana viridata* are other striking instances of minor changes. The specimens of the former from Urbana show a very much shorter posterior portion with a more rounded tail than is given in the original description; also the intestinal diverticula are not regular and straight but pointed and curved. In *Typhloplana viridata* the differences are very marked. The shape of the head region instead of being pointed is nearly as broad as any part of the body. Then, the green color is diffused thru the parenchyma fluid and not held in the color bodies alone. These examples are sufficient to show the kind of variations common among the forms of the inland ponds.

Of the species present in different localities, some occur much more widely than others. *Stenostoma leucops* seems to be almost cosmopolitan and more than any other is found in small ponds. Others, such as the genera of the Microstomidae possessing simple anatomy, are also common. It seems evident that the more primitive types adapt themselves easily to any surroundings and also that they are not so responsive to environment in the way of variation. On the other hand several members of the Typhloplanidae occur in many places. They show a greater degree of anatomical variation and are thus able to exist under diverse conditions. The two genera of the Prorhynchidae which are listed here were found only at one place and then only as a few specimens. The Dalyellids are another family not so widely scattered. So far, they have appeared in only two or three places. The question of distribution is partially one of chance and partially one of adaptability. The discussion above mentions only the general localities where the several families are found and the most prominent reason for this occurrence.

Any study of a number of families is likely to reveal certain characters of comparative interest. Perhaps the most conspicuous detail of structure in such a study of the Rhabdocoela is the shape which is at once significant and important. Within the group there is a striking similarity of form even among types differing essentially in anatomical particulars. Never long and cylindrical like the higher worms, never very flat like the related Polyclads, these worms are intermediate between the two. Some species are almost perfect in the spindle shape, large in the middle and tapering evenly toward either end, others are very nearly cigar-shaped, the head being broadened and slightly truncate. The most common variations are in the two extremities. The head may be broad or pointed, rounded or sharply angled. The posterior end often tapers very gradually making a long slender tail and often is broadened to form a heavy square spatula. Generally the anteror end is somewhat flat and the tail more or less cylindrical. Almost always the dorsal surface is elevated thru the center. Most of the group swim freely thru the open water or wriggle their way thru dense masses of filamentous algae and a spindle-shaped body is most easily propelled under such condition. The flatness of some species such as the Prorhynchidae is clearly the best shape for those types which habitually creep over smooth surfaces, as for instance the stems and leaves of aquatic plants. Here they cling closely without presenting a projecting mass by which they might be easily dislodged. Then, too, the squarely truncated head does not cause any special inconvenience, as it might in free-swimming forms. Another point which may have to do with the shape, is the entire lack of locomotor organs or projecting parts of any sort, and since the body is moved partly by muscular contraction and partly by the action of the cilia, extreme smoothness is a great advantage. As a whole, the shape is characteristic of the group and is closely related to the mode of life.

The method of locomotion has been mentioned as either by means of cilia or by muscular action, and the relative amount of development of each

depends upon the functioning of the other. There are four types of locomotion: first, free swimming movement where there is no twisting or turning of the body; second, free swimming where the whole body rolls spirally; third, a creeping or crawling over surfaces in which instances the movement may be entirely a gliding or slipping, or may be by muscular contraction; fourth, a scrambling or wriggling thru masses of silt or debris. In the first type of movement, the cilia are large and evenly distributed over the whole body and the muscular system is used only for special contraction. *Strongylostoma rosaceum* is an example of this sort. The second method, of rolling over and over, is illustrated by the habit of Stenostoma, where the spiral twisting is very marked. Again in such forms as habitually creep or crawl, the cilia are generally extremely fine while the muscular contraction of the body as a whole is well developed and is constantly used. Examples of this sort are furnished by *Macrostoma album* and the several genera of the Prorhynchidae which always cling to some surface and do not let go, so that they never swim out unprotected into the water. The different species of Mesostoma also have this same habit. These forms may be said to be lurking animals or bottom inhabitants, never found in open water. Upon occasion when hunting in a mass of algae, any form may make use of both muscular system and surface cilia in climbing around and thru tangled filaments, but generally where the activity is muscular the cilia are very small. This correlation of cilia size with muscular development is a notable one in all the rhabdocoel families.

Other characters of comparative importance are the relative thickness of integument, heavy eye pigment, and extremely specialized pharyngeal apparatus. The outline on the following page summarizes the most conspicuous points in this study.

SUMMARY

1. In swiftly flowing streams where a rocky bed furnishes a sheltered place of attachment, planarians and a few creeping rhabdocoels find a suitable location.

2. For most of the free-swimming species, ponds and temporary puddles supply the best conditions. Such a situation comprises: first, a protected retreat and also a feeding ground which may be found in a mass of filamentous algae; second, a source of food which may be found among the animal communities.

3. The response to the presence or absence of oxygen and carbon dioxide is more precise than that caused by any other stimulus.

4. The reaction to light varies in different species but in most instances is negative tho not definitely so.

5. Response to temperature is general or diffuse, rather than to a localized stimulus, as, for example, the seasonal change in the condition of the water.

6. Since nourishment is gained mostly from disintegrating protoplasm, the food relationships are very simple and altho nearly defenseless the Turbellaria seem to have few enemies.

7. The new species, *Stenostoma giganteum*, *Stenostoma glandiferum*, *Macrostoma album*, *Dalyellia alba*, *Dalyellia megacephala*, *Strongylostoma rosaceum*, *Mesostoma angulare*, *Mesostoma simplex*, are described carefully both as to structure and also as to the precise conditions of existence under which they may be expected to occur.

BIBLIOGRAPHY

BALL, STANLEY C.

1916. The Development of *Paravortex gemellipara* (*Graffilla gemellipara* Linton). Jour. Morph., 27:453-557.

CHILD, C. M.

1901. Fission and Regulation in *Stenostoma leucops*. Biol. Bull., 2:329-31.

1902. An Experimental Study of Regulation in *Stenostoma*. (Amer. Morph. Soc.) Science, n.s., 15:527-8.

1902. Studies in Regulation. I. Fission and Regulation in *Stenostoma*. Arch. Entw.-Mech., 15:187-236; 355-420; 3 pl.

1903. Studies on Regulation. II. Experimental Control of Form Regulation in Zooids and Pieces of Stenostoma. Arch. Entw.-Mech., 15:603-37; 2 pl.

1903. Studies on Regulation, III. Regulative Destruction of Zooids and Parts of Zooids in Stenostoma. Arch. Entw.-Mech., 17:1-40; 3 pl.

GRAFF, L. VON

1886. Die Turbellarien, Rhabdocoelida. Graz, 2 vol.

1903. Die Turbellarien als Parasiten und Wirte. Graz, 66 pp., 3 pl.

1905. Marine Turbellarien Orotavas und der Kusten Europas. Zeit. wiss. Zool., 83:68-148.

1911. Acoela, Rhabdocoela und Alloiocoela der Vereinigen Staaten Nordamerikas. Zeit. wiss. Zool., 99:1-108.

1913. Das Tierreich. Turbellaria II Rhabdocoelida, No. 35; 354 pp.

*JENSEN, O. S.

1878. Turbellaria ad litora Norvegiae occidentalia (Turbellaria ved Norges vestkyst). Bergen, 97 pp., 8 pl.

KEPNER, WM. A., and TALIAFERRO, W. H.

1915. Preliminary Report on Relations between the Reactions of Rhabdocoels and their Environment. (Amer. Soc. Zool.) Science, n.s., 41:473-510.

LEIDY, J.

1851. Contributions to Helminthology. Proc. Acad. Nat. Sci. Phila., 5:225.

1852. Corrections and Additions to former Papers on Helminthology. Proc. Acad. Nat. Sci. Phila., 5:288-9.

LILLIE, F. R.

1901. A Comparison of Power of Regeneration in Three Genera of Planarians. (Zool. Club Univ. Chicago) Science, n.s., 13:1026-1031.

1901. Notes on Regeneration and Regulation in Planarians. (Continued). Amer. Jour. Physiol., 6:129-41.

LINTON, E.

1910. On a New Rhabdocoel Commensal with *Modiolus plicatulus*. Jour. Exp. Zool., 9:40-137.

LUTHER, ALEX.

1904. Die Eumesostominen. Zeit. wiss. Zool., 77:1-273.

1907. Ueber die systematische Stellung der Rhabdocoelenfamilie Catenulidae s. str. Zool. Anz., 31:718-23.

MAST, S. O.

1911. Preliminary Report on Reactions to Light in Marine Turbellaria. Yearbook Carnegie Inst. Washington, 9:131-33.

MORGAN, T. H.

1898. Experimental Studies of the Regeneration of *Planaria maculata*. Arch. Entw. Mech., 7:364-97.

1899. Regeneration in *Bipalium*. Arch. Entw.-Mech., 9:563-86.

1900. Regeneration in Planarians, Arch. Entw.-Mech., 10:58-119.

*OERSTED, A. S.

1844. Entwurf einer systematischen Eintheilung und speciellen Beschreibung der Plattwürmer auf mikroskopische Untersuchungen gegründet. Copenhagen, 96 pp., 3 Tab.

OTT, H. N.

1892. A Study of *Stenostoma leucops* O. Schm. Jour. Morph., 7:263-304; 3 pl.

PATTERSON, J. T.

1912. Early Development of *Graffilla gemellipara*, A Supposed Case of Polyembryony. Biol. Bull., 22:173-204.

SCHMIDT, O.

1848. Die rhabdocoelen Strudelwürmer des süssen Wassers. Jena, 65 pp.

*SEKERA, E.

1888. Prispevky ku znamostem o turbellaruch sladkovoduich. Sitz.-ber. d. k. böhm. Ges. d. Wissensch., math.-naturw. Cl., p. 344.

SILLIMAN, W. A.

1885. Beobachtungen über die Susswasser-Turbellarien Nordamerikas. Zeit. wiss. Zool., 41:48-78.

STRINGER, CAROLINE E.

1909. Notes on Nebraska Turbellaria with Descriptions of two new Species. Zool. Anz., 34:257-262.

*ULJANIN W.

1870. Die Turbellarien der Bucht von Sevastopol. Berichte des Vereins d. Freunde d. Naturwissenschaften zu Moskau, 96 pp., 7 pl.

WALTON, L. B.

1912. The Land Planarians of North America, with a Note on a New Species. (Amer. Soc. Zool.) Science, n.s., 35:940.

WILHELMI, J.

1908. On the North American Triclads. Biol. Bull., 15:1-6.

WOODWORTH, W. McM.

1897. On Some Turbellaria from Illinois. Bull. Mus. Comp. Zool. Harvard Coll., 31:1-16.

1896. On the Identity of *Procotyla fluviatilis* Leidy and *Dendrocoelum lacteum* Oersted. Amer. Nat., 30:1048-9.

*Original papers not seen.

YOUNG, R. T.
1912. The Epithelium of Turbellaria. Jour. Morph., 23:255-68.

ZACHARIAS, OTTO
1902. Eine neue Turbellarienspecies (*Stenostomum turgidum*). Zool. Anz., 26:41-2.

EXPLANATION OF PLATES

ABBREVIATIONS

b	brain	*m*	mouth
bf	body fold	*n*	nucleus
c	cilia	*o*	ovary
com	commissure	*p*	pigment
cp	ciliated pit	*par*	parenchyma
cs	cirrus sac	*ph*	pharynx
cyt	cytoplasm	*pi*	zoochlorellae
e	eye	*rk*	rhabdites
ep	epithelium	*r sem*	receptaculum seminalis
fl	flame cell	*s cell*	sensory cell
gp	genital pore	*sp*	sperm cell
int	intestine	*t*	testis
int con	intestinal constriction	*u*	uterus
int gl	intestinal glands	*vit*	yolk glands
int pr	intestinal prolongation	*vs*	ventral surface
lrf	light refracting organ	*wp*	protonephridium

PLATE I

EXPLANATION OF PLATE

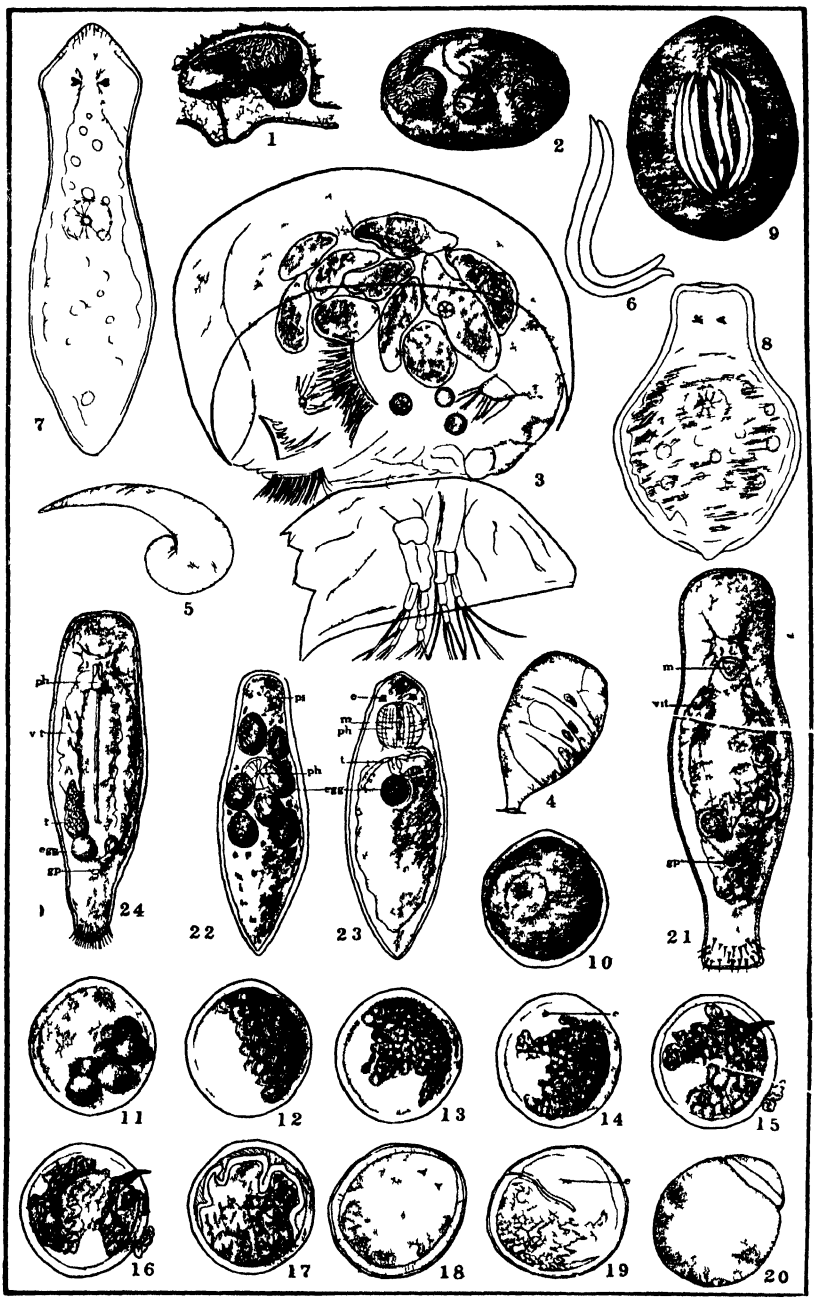
(Figures 1 to 9 represent *Strongylostoma rosaceum*)

Fig. 1.—Reproductive organs, lateral view; × about 150.
Fig. 2.—Reproductive organs, dorsal view; × about 150.
Fig. 3.—Cyclops shell with worms feeding within; × about 10.
Fig. 4.—Ovary, camera lucida; × 67.
Fig. 5.—Testes; × about 67.
Fig. 6.—Rhabdites lying free, camera lucida; × 50.
Fig. 7.—Diagram of worm extended; × about 60.
Fig. 8.—Diagram of worm contracted; × about 60.
Fig. 9.—Cell with rhabdites, camera lucida; × 50.

(Figures 10 to 20 were drawn with camera lucida and show eggs of *Strongylostoma rosaceum* in various stages)

Fig. 10.—Egg in one-cell stage; × 67.
Fig. 11.—Eight-cell stage; × 67.
Fig. 12.—About thirty-two-cell stage; × 67.
Fig. 13.—Gastrula nearly complete; × 67.
Fig. 14.—About fifth day; × 67.
Fig. 15.—At 9:56 A.M. in process of turning; × 67.
Fig. 16.—At 10:08 A.M. rotated 180°; × 67.
Fig. 17.—Seventh day, much folded; × 67.
Fig. 18.—Eighth day, dorsal view; × 67.
Fig. 19.—Eighth day, lateral view; × 67.
Fig. 20.—Ninth day, empty shell; × 67.

Fig. 21.—*Macrostoma album*, slightly compressed; × about 50.
Fig. 22.—*Typhloplana viridata*, slightly compressed; × about 80.
Fig. 23.—*Dalyellia megacephala*, slightly compressed; × about 27.
Fig. 24.—*Dalyellia alba*, slightly compressed; × about 40.

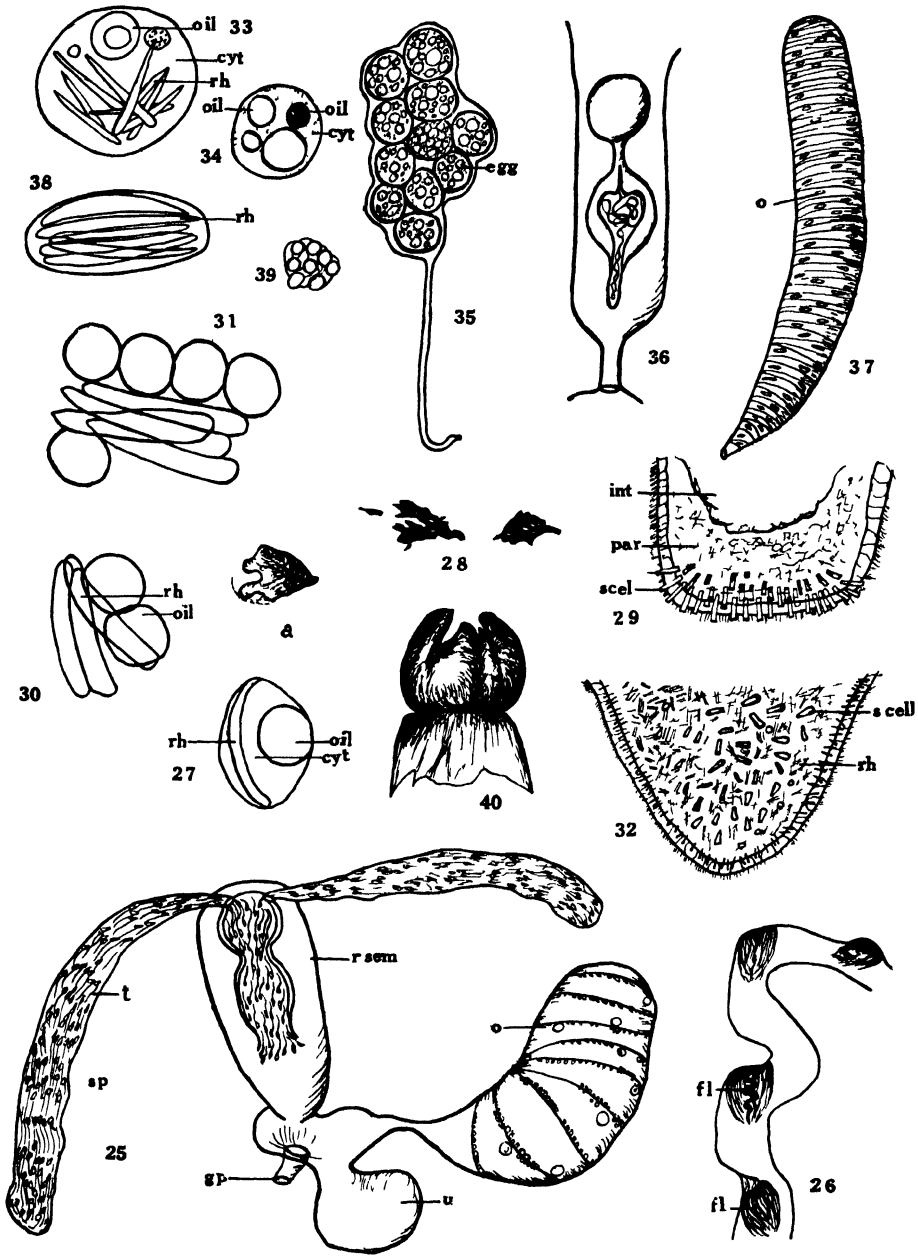


HIGLEY TURBELLARIA FROM THE MISSISSIPPI BASIN PLATE I

PLATE II

EXPLANATION OF PLATE

Fig. 25.—Reproductive organs of *Dalyellia megacephala*; × about 200.
Fig. 26.—Protonephridium of *Dalyellia alba*; × about 340.
Fig. 27.—Rhabdites of *Typhloplana viridata*, one in cell. Camera lucida; × 350.
Fig. 28.—Eyes of *Strongylostoma rosaceum*; × about 200.
a. Lateral surface of eye; × about 200.
Fig. 29.—Tail region of *Mesostoma angulare*; × about 100.
Fig. 30.—Rhabdites of *Typhloplana viridata*. Camera lucida; × 350.
Fig. 31.—Rhabdites of *Typhloplana viridata*, old cell; × about 300.
Fig. 32.—Tail region, *Mesostoma simplex*; × about 100.
Fig. 33.—Rhabdites in cell, *Mesostoma simplex*. Camera lucida; × 150.
Fig. 34.—*Mesostoma simplex*, vitelline gland cell, showing stored oil globules; × about 250.
Fig. 35.—Ovary of *Mesostoma simplex*; × about 350.
Fig. 36.—Cirrus sac, *Mesostoma simplex*; × about 350.
Fig. 37.—Testis, *Mesostoma simplex*; × about 350.
Fig. 38.—Rhabdites in cell, *Mesostoma simplex*; × about 200.
Fig. 39.—Eye, *Dalyellia megacephala*; × about 175.
Fig. 40.—End view of rhabdite-bearing cell of *Mesostoma simplex*; × about 350.

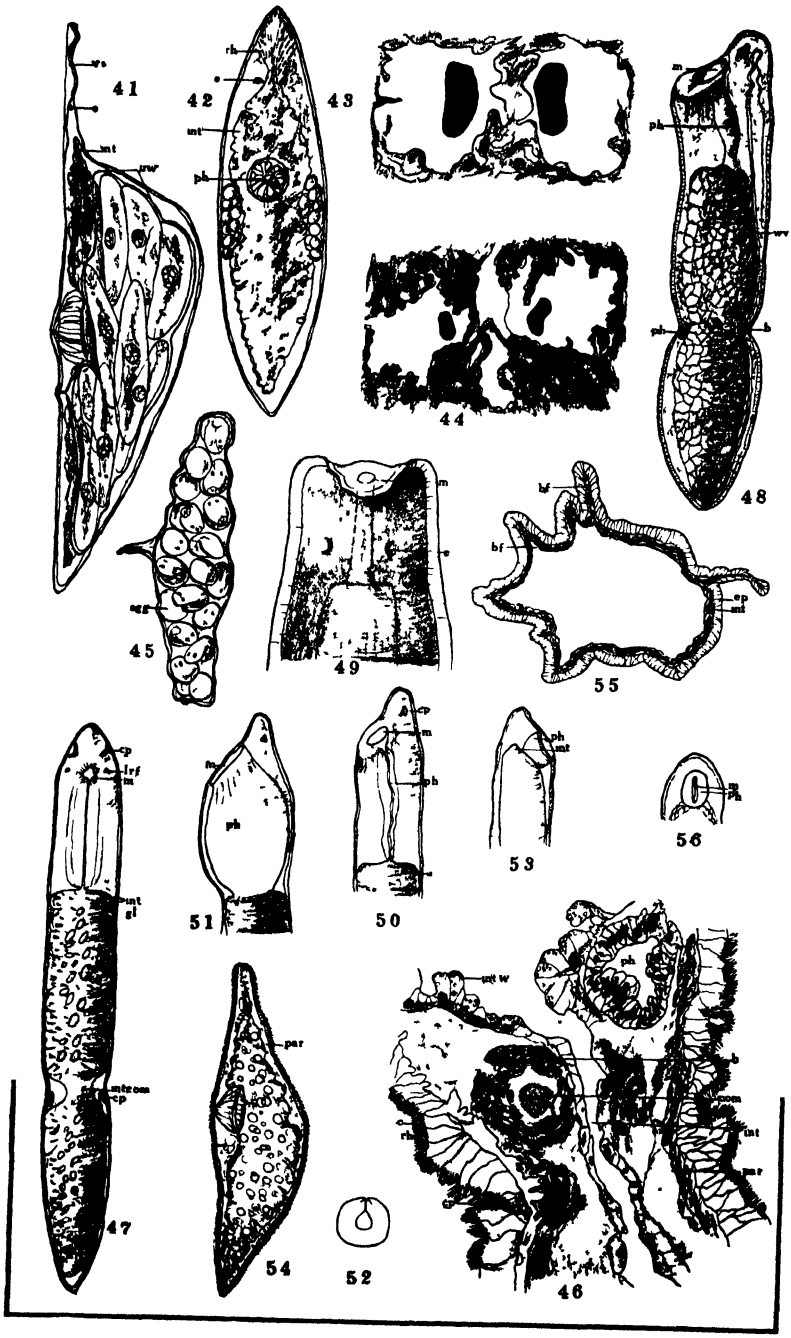


HIGLEY — BELLARIA FROM THE MISSISSIPPI BASIN PLATE II

PLATE III

EXPLANATION OF PLATE

Fig. 41.—*Mesostoma angulare*, lateral view, slightly compressed; × 35.
Fig. 42.—*Mesostoma simplex*, slightly compressed; × 26.
Fig. 43.—Eyes of *Planaria maculata*; × about 67.
Fig. 44.—Eyes of *Planaria maculata*, camera lucida; × 67.
Fig. 45.—Uterus of *Mesostoma angulare*, showing young worms and eggs just ready to hatch. × about 35.
Fig. 46.—Section thru fission plane of *Stenostoma giganteum*. Camera lucida; × 50.
Fig. 47.—*Stenostoma glandiferum*, dorsal view, slightly compressed; × about 90.
Fig. 48.—*Stenostoma giganteum*, lateral view slightly compressed; × 60.
Fig. 49.—Head of *Dalyellia dodgei*, antero-dorsal view, showing elevated mouth; × about 70.
Fig. 50.—Head of *Stenostoma leucops*, pharynx closed; × about 67.
Fig. 51.—Head of *Stenostoma leucops*, pharynx open; × about 67.
Fig. 52.—Nematocyst of *Microstoma caudatum*; × about 850.
Fig. 53.—Lateral view of head of *Microstoma caudatum*; × about 67.
Fig. 54.—*Strongylostoma rosaceum*, lateral view, slightly compressed; × about 50.
Fig. 55.—Transverse section, *Mesostoma angulare*, showing folds of body wall. Camera lucida; × 170.
Fig. 56.—Ventral view of head of *Microstoma caudatum*; × about 67.



HIGLEY TURBELLARIA FROM THE MISSISSIPPI BASIN PLATE III

ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. IV April, 1918 No. 4

EDITORIAL COMMITTEE

STEPHEN ALFRED FORBES WILLIAM TRELEASE

HENRY BALDWIN WARD

PUBLISHED UNDER THE
AUSPICES OF THE GRADUATE SCHOOL BY
THE UNIVERSITY OF ILLINOIS

COPYRIGHT, 1918 BY THE UNIVERSITY OF ILLINOIS
DISTRIBUTED MAY 31, 1919

NORTH AMERICAN PSEUDOPHYLLIDEAN CESTODES FROM FISHES

WITH THIRTEEN PLATES

BY

ARTHUR REUBEN COOPER

Contributions from the
Zoological Laboratory of the University of Illinois
under the direction of Henry B. Ward, No 127

COPYRIGHT, 1919
BY THE UNIVERSITY OF ILLINOIS

TABLE OF CONTENTS

	Pages
Introduction	7
Historical Data	8
Explanation of Terms	10
Key to the Families, Subfamilies, Genera and Species	11
Order PSEUDOPHYLLIDEA	13
Family DIPHYLLOBOTHRIIDAE	15
Ligulinae Lühe 1899	16
Ligula Bloch 1782	17
Ligula intestinalis (Linnaeus 1758)	18
Schistocephalus Creplin 1829	30
Schistocephalus solidus (O. F. Müller 1776)	30
Haplobothriinae Cooper 1917	42
Haplobothrium Cooper 1914	43
Haplobothrium globuliforme Cooper 1914	44
Cyathocephalinae Lühe 1899, e. p.	53
Cyathocephalus Kessler 1868	53
Cyathocephalus americanus Cooper 1917	53
Bothrimonus Duvernoy 1842	62
Bothrimonus intermedius Cooper 1917	63
Marsipometrinae Cooper 1917	70
Marsipometra Cooper 1917	70
Marsipometra hastata (Linton 1897)	71
Triaenophorinae Lühe 1899	81
Triaenophorus Rudolphi 1793	81
Triaenophorus sp. larv	82
Fistulicola Lühe 1899	88
Fistulicola plicatus (Rudolphi 1819)	89
Family PTYCHOBOTHRIIDAE	93
Ptychobothriinae Lühe 1899	94
Bothriocephalus Rudolphi 1808	95
Bothriocephalus scorpii (Müller 1776)	96
Dibothrium angustatum (Rudolphi)	112
Bothriocephalus claviceps (Goeze 1782)	114
Bothriocephalus cuspidatus Cooper 1917	123
Bothriocephalus manubriformis (Linton 1889)	133
Dibothrium laciniatum (Linton)	145
Bothriocephalus histiophorus (Shipley)	147
Bothriocephalus occidentalis (Linton 1898)	149
Clestobothrium Lühe 1899	153
Clestobothrium crassiceps (Rudolphi 1819)	154
Amphicotylinae Lühe 1902	171
Abothrium van Beneden 1871	171
Abothrium rugosum (Batsch 1786)	172
Abothrium crassum (Bloch 1779)	186

Bibliography 201
Explanation of Plates 211
Index of Hosts 237
Index 241

INTRODUCTION

Soon after commencing the study of *Haplobothrium globuliforme* Cooper the writer (1914, 1914a) saw that, apart from the early and somewhat brief reports and descriptions by Leidy and the later, but yet pioneer work of Linton on both marine and fresh-water species, very little had been done on the members of the order in America. Consequently the desire for an opportunity to work up other species which had in the meantime been collected at the Canadian Lake Biological Station on Georgian Bay, located at Go-Home Bay, Muskoka District, Ontario, and at the Marine Biological Station at St. Andrews, New Brunswick, grew with the feeling that something of a comprehensive nature ought to be undertaken in order not only to ascertain to what extent European species are to be found in this continent, but also to locate properly in the classification at least some of the new forms formerly described, especially by Linton. Altho the material then at hand was investigated to a certain extent at the University of Toronto, it was not until the writer came to the University of Illinois that it was studied at all thoroly with the aid of other material for comparison from the collection of the University of Illinois, under the care of Professor Henry B. Ward.

Supplementary material, which in many cases was all that was available, was obtained by Professor Ward from the United States National Museum and the Bureau of Animal Industry, but apart from a few vials no European specimens could be procured, owing to the present international conflict. On account of the lack of the latter most of the determinations have been made with the aid of the literature only, a fact which the writer feels may necessitate future changes in connection with a few species which have been more or less tentatively regarded to be the same as those in Europe. In all cases, however, the specific details of the American forms have been emphasized, so that if changes have to be made later, the basis for such will be at hand. The writer would like to point out in this connection the comparative lack from a systematic standpoint of adequate descriptions of many of the European species which have been known for many years. It was this fact which in the absence of the original material for comparison made the present work one attended with not a little difficulty.

In the main the classification of the order adopted by the writer is that proposed by Lühe (1902) and later (1910) retained with only a few modifications. The family of the Caryophyllaeidae is, however, not included, so that the order is considered to be rather that of Carus (1863), with Lühe's later conceptions of the other families. One of the latter must now again be modified considerably owing to the present study of two quite aberrant species, namely, *Haplobothrium globuliforme* Cooper and *Marsipometra hastata* (Linton) which have been found by the writer to be very disturbing to the classification.

The writer wishes here to tender his thanks in the first place to the Biological Board of Canada for placing means and facilities at his disposal in connection

with his earlier collecting at the above-mentioned Canadian Biological Stations; to the University of Illinois for the opportunity of collecting further material at the Marine Biological Laboratory at Woods Hole, Massachusetts, and at the Harpswell Laboratory, South Harpswell, Maine, during the summer of 1916, and to the staffs of these institutions as well as to that of the Marine Laboratory of the United States Bureau of Fisheries at Woods Hole for assistance and direction in connection with the same; to the Smithsonian Institute and the Bureau of Animal Industry, from whom valuable material was obtained for comparison, in the latter case thru the kind offices of Dr. C. W. Stiles of the Hygienic Laboratory, Washington; and to the following investigators for alcoholic specimens: Professor O. Fuhrmann, University of Neûchatel, Switzerland, Professor Edwin Linton, Washington and Jefferson College, Professor E. M. Walker, University of Toronto, Dr. H. J. VanCleave, University of Illinois, Dr. G. R. LaRue, University of Michigan, Dr. A. S. Pearse, University of Wisconsin, and Messrs. H. R. Hill and R. P. Wodehouse.

Finally to Professor H. B. Ward the writer wishes to express his sincere indebtedness not only for the use of his extensive private library and collections and for the procuring of rare books and specimens, but for his constant and stimulative interest in, and valuable criticism of, the work which has resulted in the following paper.

HISTORICAL DATA

Apart from Gmelin's (1790) collecting together the data given by the older writers such as Linnaeus, Pallas, Müller, Goeze, Bloch, Fabricius, Batsch, Schrank and Abildgaard, and Zeder's (1800, 1803) treatises, the first most important work on the bothriocephalid cestodes was the *Entozoorum Historia Naturalis* by Rudolphi (1808-1810). In this he reviewed the earlier literature, making valuable comments on the same, and described species of Ligula, Triaenophorus and Bothriocephalus, the latter name being used for the first time. While Lamarck (1816) dealt with only the more common species, Rudolphi in his second work of major importance, the *Entozoorum Synopsis* (1819), made some corrections of his earlier publication and further contributions in the way of a few new species. F. S. Leuckart (1819), who did not receive Rudolphi's *Entozoorum* until after his own work was in print, dealt only with species of the genus Bothriocephalus as conceived by Rudolphi, which then contained members not only of the Pseudophyllidea but also of the Tetraphyllidea and the Trypanorhyncha. Nitzsch (1824) briefly defined the species of the same genus, while later Creplin (1839) dealt with them more in detail and erected the new genus Schistocephalus. Drummond (1838) was one of the first to report bothriocephalids from the British Isles, while Bellingham (1844) and Thompson (1844) made further contributions, all three dealing with forms from Ireland. Eschricht (1841) published some of the earliest data on the internal anatomy of the group, and Kölliker (1843) made a study of the development of the eggs of a few species. The next and perhaps most important work was that by Dujardin (1845) who, while following Rudolphi in the

main, made many valuable additions from original observations. Van Beneden (1849, 1850) first essayed to erect a more comprehensive classification than had hitherto been used, and Diesing (1850) went much farther in his Subtribe I, Gymnobothria, of Tribe IV, Bothriocephalidea, of Suborder I, Aprocta, of Order IV, Cephalocotylea. Baird (1853) reverted to Rudolphi's brief system, in listing forms from the British Museum. Wagener in two papers (1854, 1857) published studies on the development which even to-day are models of careful work and excellent illustrating. Leidy (1855, 1856) was the first to report forms from America, while Weinland (1858) made a few references to bothriocephalids.

Then, until Diesing (1863) revised his classification nothing of systematic importance appeared. Olsson (1867) was one of the first to report species from the Scandinavian countries; later (1876, 1893) he made further contributions from the same region. After Willemoes-Suhm's (1869) studies on the development of *Schistocephalus dimorphus*, came Duchamp's (1876) and Donnadieu's (1877) classical experiments on the life-histories of the ligules. Linstow (1878) brought together in a list the forms known up to that time. A few years later Fraipont (1880, 1881) published studies on the excretory system of a number of species which even to-day are perhaps the most important contributions in that direction. The nervous system was made the object of special inquiry by Lang (1881), while later it was dealt with more at length by Niemiec (1888) and Cohn (1898). After a period in which such works as those with studies on development by Moniez (1881), Zschokke (1884) and Schauinsland (1885) are prominent, come the next reports of species from America, namely, those contained in Linton's first paper (1889). The latter was followed by a second (1890), containing extensions of the first, and later by others (1891, 1897, 1901 and 1901a) dealing with a variety of forms from marine and fresh-water fishes. Further anatomical studies by Lönnberg (1891), Kraemer (1892), Matz (1892) and Zernecke (1895) lead on to Monticelli's (1892) classification, which was the most important since the time of Diesing, altho Perrier (1878) had in the meantime voiced his ideas along that line. The next in order is Ariola's (1896) division of the family "Bothriocephalidae," in which incidentally were yet to be found errors regarding the position of the bothria.

Beginning with 1894 and continuing to 1900 there was in progress the publication of Braun's Cestodes in Bronn's Tierreich, which is by far the most comprehensive work on the group, since it brings together the substance of the most important of the earlier works on the morphology as well as the system of the order. One of the first papers by Lühe, who did recent important work on the group, was that (1896) in which he dealt with the nervous system of Ligula. Further study led him to publish a few years later (1899) his first classification, which was adopted by Braun (1894-1900). In the meantime Lönnberg (1897) made valuable contributions to the knowledge of the phylogeny of the parasitic flatworms; while Gamble (1896) and Perrier (1897) had erected systems of classification which, however, do not have nearly as much in their

favor for general acceptance as does that by Lühe. In 1900 Ariola brought out his revision of the family of the Bothriocephalidae, which, however, was shown by Lühe (1901) to be rather of the nature of a compilation, involving at the same time several omissions, than a distinct advance in our knowledge. In 1901 there appeared in Lankester's Treatise on Zoology Benham's classification of Cestodes which professedly follows the earlier works of Railliet and Blanchard. Lühe's (1902a) revision of the bothriocephalid system comes next in order. It is this newer system, only slightly modified in 1910, that is accepted by the writer with several necessary modifications which are dealt with below.

From 1902 until Die Süsswasserfauna Deutschlands was published, the literature on the group consists mostly of papers on individual species or mere listings. Spengel's (1905) paper on Die Monozootie der Cestoden ought, however, to be mentioned, since it is one of the latest discussions of a question which occupied a good deal of the attention of many of the older writers. Finally Ward (1910) and the writer (Cooper, 1914a, b) made the latest additions to the American literature, while Stiles and Hassall won the gratitude of the younger workers at least by their publication of the section of the Index-Catalogue of Medical and Veterinary Zoology on Subjects: Cestoda and Cestodaria which the writer has found of inestimable value in the pursuit of his studies.

EXPLANATION OF TERMS

Owing to the fact that not a little confusion exists in the earliest literature regarding the terms of orientation used for the cestode body, the writer wishes here to explain those that will be employed in the specific descriptions below.

Even much later than the time of Diesing (1850) the word "lateral" was used to refer to the flat surfaces of the typical strobila, while "marginal" was and is even yet perfectly clear in meaning; but from the standpoint of bilateral symmetry both words may mean the same thing. Here they are considered to be synonymous and are used to refer to any part which is situated in or at the edges of the strobila and consequently of the individual proglottides. On the other hand, the word "surficial" is adapted from geology to take the place of the word "flächenstandig" which is used freely in Lühe's papers to mean that the structures in question are located on the broad, flat surfaces of the chain. As is customary, the latter are considered to be dorsal and ventral in position, the ventral surface being that which is nearer the isthmus of the ovary. The end bearing the scolex is called the anterior end and the opposite, the posterior end, despite differences of opinion as to which is which. For the sake of brevity the words, "length," "depth" and "breadth" (or "width") are used instead of the longer terms, diameters in the longitudinal, in the dorsoventral and in the transverse directions, respectively, excepting where the organ in question, e.g., the transversely elongated cirrus-sac of the Triaenophorinae, is so shaped that it would be confusing to speak of its obvious length as its width. Otherwise the usual terms of orientation are employed.

KEY TO FAMILIES, SUBFAMILIES, GENERA AND SPECIES

OF PSEUDOPHYLLIDEA FROM FISHES DESCRIBED IN THIS PAPER

1 (14, 15) Eggs with thick shells and opercula. Opening of cirrus and vagina on the same surface as that of the uterus and ahead of it or marginal.
Family DIPHYLLOBOTHRIIDAE Lühe 1910 . . 2

2 (11) Opening of cirrus and vagina surficial 3

3 (8) Genital openings always on the same surface of the strobila . . 4

4 (7) Scolex very short, not distinct from the strobila.
Subfamily LIGULINAE Lühe 1899 . . 5

5 (6) Segmentation confined to the anterior end, or (in larvae) absent . . . . . Ligula Bloch 1782
Type and only species: *L. intestinalis* (Linnaeus 1758) . . p. 18

6 (5) Segmentation complete even in the larval stages.
Schistocephalus Creplin 1829
Type and only species.
Schistocephalus solidus (O. F. Müller 1776) . . . . p. 30

7 (4) Scolex (secondary, see below) similar in shape to the first proglottis; no neck; segmentation beginning immediately behind the scolex, but confined to the anterior end of the worm.
Subfamily HAPLOBOTHRIINAE Cooper 1917 . . p. 42
Type and only genus . . Haplobothrium Cooper 1914 . . p. 43
Type and only species: *H. globuliforme* Cooper 1914 . . p. 44

8 (3) Genital openings of different segments not on the same surface, but alternating irregularly from one surface to the other. External segmentation little expressed.
Subfamily CYATHOCEPHALINAE Lühe 1899 . . 9

9 (10) Scolex an unpaired, terminal, funnel-shaped organ.
Cyathocephalus Kessler 1868
Only American species: *C. americanus* Cooper 1917 . . p. 53

10 (9) Scolex with two almost spherical bothria, the apertures of which may be separated or more or less completely fused to form a single terminal opening . . . . Bothrimonus Duvernoy 1842
Only American species: *B. intermedius* Cooper 1917 . . p. 63

11 (2) Opening of cirrus and vagina marginal.
Subfamily TRIAENOPHORINAE Lühe 1899 . . 12

12 (13) Scolex armed with four three-pointed hooks.
Triaenophorus Rudolphi 1793
Only larval forms of two specific types present . . . . . p. 82

13 (12) Scolex sagittate, or replaced by a pseudoscolex. Segmentation strongly expressed, the individual proglottides very short with leaf-like free lateral portions . . . . . Fistulicola Lühe 1899
Only American species: *F. plicatus* (Rudolphi 1819) . . . p. 89

14 (1, 15) Eggs with thin shells and no opercula. Opening of cirrus and vagina marginal, that of uterus at the same level or slightly behind it and ventral. Segmentation very distinct and regular.
Subfamily MARSIPOMETRINAE Cooper 1917 . . p. 70
Type and only genus: Marsipometra Cooper 1917 . . p. 70
Type and only species: *M. hastata* (Linton 1898) . . p. 71

15 (1, 14) Eggs with thin shells and no opercula. Opening of cirrus and vagina dorsal and behind the ventral uterus-opening, or marginal in which case sementation is not well expressed.
Family PTYCHOBOTHRIIDAE Lühe 1902 . . 16

16 (27) Opening of cirrus and vagina surficial.
Subfamily PTYCHOBOTHRIINAE Lühe 1899 . . 17

17 (26) Scolex elongated, with prominent terminal disc. Segmentation well developed, neck absent.
Bothriocephalus Rudolphi 1808 . . 18

18 (23) Scolex not pronouncedly constricted posteriorly 19

19 (20) Uterus-sac occupies one-sixth of the transverse diameter of the proglottis . . . . . *B. scorpii* (Müller 1776) . . p. 96

20 (19) Uterus-sac occupies one-third of the transverse diameter of the proglottis 21

21 (22) Scolex small . . . . . *B. claviceps* (Goeze 1782) . . p. 114

22 (21) Scolex large, terminal disc deeply notched surficially, sagittate in lateral view . . . . . *B. cuspidatus* (Cooper 1917) . . p. 123

23 (18) Scolex constricted posteriorly 24

24 (25) Terminal disc deeply notched laterally as well as surficially; vagina provided with a bulbous sphincter near its opening . . . . . *B. manubriformis* (Linton 1889) . . p. 133

25 (24) Terminal disc rectangular; no vaginal sphincter . . . . . *B. occidentalis* (Linton 1898) . . p. 149

26 (17) Scolex almost spherical; walls of each bothrium fused to form a hollow organ of attachment with a small anterior opening
Clestobothrium Lühe 1899
Type and only species: *C. crassiceps* (Rudolphi 1819) . . p. 154

27 (16) Opening of cirrus and vagina marginal.
Subfamily AMPHICOTYLINAE Lühe 1902 . . 28
Onlygenus represented . . . . . Abothrium van Beneden 1871.

28 (29) Pseudoscolex in adult. Longitudinal muscles in bundles. Vitelline follicles entirely within the longitudinal muscles.
A. rugosum (Batsch 1786) . . p. 172

29 (28) Scolex typical, but variously shaped. Longitudinal muscles not in bundles. Vitelline follicles among the longitudinal muscles or outside of them . . . . . *A. crassum* (Bloch 1779) . . p. 186

Order PSEUDOPHYLLIDEA Carus 1863, nec Lühe 1910, e. p.

Polyzootic cestodes with mostly unarmed scolex without rostellum or proboscis formation, excepting in the Haplobothriinae where the primary scolex is provided with four protrusible proboscides resembling those of the Trypanorhyncha. Usually with two weakly developed sucking grooves, which in individual cases are modified by the strong development of their walls or by more or less extensive fusion of their edges, so that they may appear funnel-shaped or tubular, which may also unite with each other more or less completely to form an unpaired terminal adhesive organ, or become rudimentary or entirely absent, in which latter case they are replaced by a terminal functional organ of attachment. The development of a pseudoscolex takes place occasionally. External segmentation more or less pronounced, only seldom completely absent. Genitalia in each segment usually single, seldom double. Their development proceeds from ahead backwards and does not continue to a degeneration of the reproductive glands; but the majority of the proglottides, being at the same stage of development, bring their sexual products to maturity at the same time, so that in all of them new eggs are formed continuously and all the eggs of the whole animal are at the same stage of embryonic development. A surficial opening of the uterus is always present.

Testes numerous; vas deferens strongly coiled, without a true seminal vesicle. Ovary near the posterior end of the proglottis, mostly median in the case of single genitalia, seldom approaching the margin of the strobila bearing the genital opening (that of the cirrus and vagina). Vitelline follicles very numerous, mostly in the cortical, seldom in the medullary parenchyma. Uterus a more or less winding canal, the individual coils of which converge somewhat towards the centre of the proglottis to form the so-called rosette; but in other forms it enlarges to form a capacious cavity, the uterus-sac, from which the duct-like beginning of the uterus is sharply separated. Eggs operculate or non-operculate, developing mostly only after being laid, but in other cases within the uterus.

The above diagnosis of the order is that of Lühe (1910:11), minus the family Caryophyllaeidae and partly emended to accommodate the subfamily Haplobothriinae, in which what is here considered to be the true (or primary) scolex is deprived of bothria but provided with four eversible proboscides quite comparable in structure to those of the order Trypanorhyncha. It is evident that what was formerly (Cooper, 1914, 1914a) called the scolex of Haplobothrium cannot now be considered to be a true scolex but only the foremost segment of the adult or secondary strobila, which is indicated by its resemblance internally as well as externally to the segments immediately following. Whether or not a pair of bothria were originally present or are present in the very earliest stages, whether such bothria have become modified into the proboscides, or whether the latter have developed from four separate "accessory

suckers" as believed by Pintner (1880) to be the case in the Trypanorhyncha, must remain mere suggestions for the present. Furthermore as to the formation of segments there are in Haplobothrium not only conditions quite similar to those in Bothriocephalus *s. str.* and other genera in which there is no neck, segmentation beginning immediately behind the scolex, but those reminding one of the proliferation of scolices in echinococcus. In the former, as will be seen below where the process is described more in detail (p. 102), a primary segment divides up into secondary segments, these into tertiary segments, and so on until there may be eventually thirty-two or more genital segments corresponding to one primary segment formed immediately behind the scolex. In Haplobothrium a primary strobila divides up into primary segments, these subdivide into secondary segments, the definitive joints of the ordinary strobila met with, which in turn may be subdivided again and evidently indefinitely to form new chains. The chief difference between these two cases is one of degree of regularity in the subdivision. Whereas in Bothriocephalus the whole anterior region of the worm is affected, evidently no division taking place after the rudiments of the reproductive organs have become separated from the common rudiment, and the subsegments remain attached to one another, in Haplobothrium not only do the primary segments separate as secondary strobilas, but in the latter only a limited region is involved in further subdivision. On the other hand there is somewhat of a resemblance between this manner of subdivision in Haplobothrium and that of the larval Echinococcifer in that the strobilas are developed from an original "nurse." That is, the primary strobila of the former might be looked upon as a nurse from which are developed segments, comparable to the daughter-cysts of an echinococcus, which in turn produce (secondary) scolices and eventually strobilas. In other words there might be recognized at first sight a sort of alternation of generations in the case of Haplobothrium. But this comparison is only a superficial one, for as will be shown below (under Haplobothriinae) the secondary scolex cannot be considered to be a true scolex nor the secondary strobila a true strobila; but the primary strobila with its four proboscides must be regarded as such. Finally, this peculiar method of segmentation reminds one of the asexual budding of some of the oligochaete worms, particularly as regards the proliferation of subsegments in the anterior region of the first formed divisions; but further than this the comparison can scarcely be carried.

DIPHYLLOBOTHRIIDAE Lühe 1910, char. emend.

Polyzootic Pseudophyllidea with unarmed or (seldom) armed scolex. Surficial bothria variously developed; they may be modified to form sucking tubes, each with an anterior and a posterior opening, thru the growth together of their free edges, or an unpaired terminal organ of attachment can serve as a functional substitute for the rudimentary bothria or result from the more or less complete fusion of both bothria. The whole scolex may be replaced in sexually mature specimens by a pseudoscolex; or it may be (Haplobothriinae) provided with four protrusible proboscides. Neck present or absent. External segmentation mostly present, seldom absent. Genital organs numerous, mostly single in each proglottis, seldom double. Cirrus unarmed (excepting in Haplobothrium), with cleft cuticula. Opening of cirrus and vagina surficial or marginal; in the first case always on the same surface as the uterus opening and ahead of this as well as always in the median line of the genital complex, also in the median line of the proglottis in the case of single genitalia. Both surfaces of the chain of proglottides, apart from the genital openings, similarly shaped. Receptaculum seminis formed by a local enlargement of the vagina near its inner end, which as a rule is sharply separated from the spermiduct (terminal portion of the vagina). Uterus, a long, more or less winding canal, usually in the form of a rosette, formed by almost transversely directed coils crossing the median line. It may be locally more or less enlarged, but seldom forms an undivided uterus-sac distinct from the uterine duct, as in the Ptychobothriidae. Eggs thick shelled, with opercula, excepting in the Marsipometrinae; their formation is carried on continuously in fully-developed proglottides; embryonal development takes place usually after liberation, seldom in the uterus, in which case, however, all stages are found side by side.

Parasites of vertebrates.

Lühe's (1910:16) diagnosis is here emended to include the new subfamilies Haplobothriinae and Marsipometrinae. In the former not only is the scolex radically different from that of any other member of the family, but the cirrus is armed with minute spines and there is a distinct uterus-sac, separate from the uterine duct as in the Ptychobothriidae; while in the latter there is likewise a uterus-sac and the eggs are not provided with opercula. The cirrus of Haplobothrium, however, would seem to exclude the genus from the family Ptychobothriidae as well as from the Diphyllobothriidae, since it is not "unarmed, with cleft cuticula," but provided with minute yet distinct cuticular spines bearing some resemblance to those of the Acanthophallidae (Amphitretidae), as pointed out elsewhere by the writer (1914:3). But *H. globuliforme* is otherwise so nearly related to *Diphyllobothrium latum* that it does not seem wise to remove it from the family on this account, especially since these spines are so minute and since the evidence points to their being probably of little, if any, functional importance. The uterus on the other hand is quite diff-

erent from that of any of the members of this family in that it is distinctly divided into uterine duct and uterus-sac as in the Ptychobothriidae. It is true that in the genus Scyphocephalus one or two of the coils of the uterine rosette becomes much enlarged when the organ is filled with eggs, while in Bothridium, as stated by Lühe (1899:49), "Der Uterus bildet keine Rosettenform, lässt jedoch Uteringang und Uterus s. str. deutlich unterscheiden; letzterer stellt gewissermassen eine zweitheilige Uterushöhle dar, indem zwei hinter einander gelegene grosse Hohlräume durch einen kurzen und dünnen Canal miteinander in Verbindung stehen." But in neither case is there a single uterus-sac, distinct and separate from the uterine duct or beginning of the uterus, but only a modified rosette formation. Roboz (1882:282) in describing the development of the uterus of *Bothridium pithonis* said that: "In dieser Weise ist er natürlich nur in jüngeren Gliedern entwickelt, während er dort, wo die Befruchtung schon beendet ist, in Folge der immer stärkeren Ansammlung von den mit chitinöser Hülle umgebener Eiern immer grösser wird und sich schliesslich zu einem die ganze Mittelschicht ausfüllenden Sack ausbreitet." It would thus seem to be comparable to that of the Ptychobothriidae in that its functional sac is developed by a distal enlargement of the original duct which gradually encroaches upon the medulla, but evidently there is no separation of the organ into two distinct parts at any stage as there is in Haplobothrium. And, as emphasized elsewhere by the writer, this separation is present at all stages in the development of the organ, which as a matter of fact proceeds in quite the same manner as that of Bothriocephalus. In Marsipometra, on the other hand, even tho the sac is formed in the same way, it is never very sharply separated from the uterine duct, altho such appears to be the case in the adult. Reference to the specific description below will elucidate this latter point. Finally as regards the fact that its eggs are not provided with opercula, Marsipometra stands alone. This character would place it at once in the Ptychobothriidae, but it is otherwise so closely related to the subfamily Triaenophorrinae that the family is here emended to accommodate it. Thus it is seen that on account of these two isolated genera the two families Diphyllobothriidae and Ptychobothriidae are much more closely related than was formerly thought to be the case.

LIGULINAE Lühe 1899

Scolex unarmed, very short, almost triangular, with anterior end, more or less drawn out into a point according to the state of contraction, passing directly into the chain of proglottides or the similarly shaped unjointed body; surficial bothria small, weakly developed. Neck absent. Formation of proglottides complete, confined to the anterior end or (in young animals) absent. Posterior end rounded. Nervous system distinguished by a large number of plexus-forming longitudinal nerves near both chief strands. Genital organs in sexually mature individuals completely developed close behind the scolex. Genital openings surficial, ventral, lying behind or near one another and near the median line. Testes in a simple dorsal layer in the lateral fields of the medul-

lary parenchyma, for the most part lateral to the nerve strands. Ovary and shell-gland median, the former ventral, the latter dorsal. Vitelline follicles in the form of a mantle in the cortical parenchyma. Vas deferens enlarged to a muscular bulb before entering the cirrus-sac. Receptaculum seminis large, sharply separated from the short and narrow spermiduct.

Sexually mature in the intestines of water birds; present as larvae in the body-cavities of teleosts where they grow quite large and develop the rudiments of the reproductive organs; occasionally also observed free in the water which they reach by the rupture of the greatly distended body-wall of the intermediate host.

Type genus: Ligula Bloch

In the above diagnosis of the subfamily by Lühe (1910:17) the statement that the testes are "in einfacher dorsaler Schicht den Seitenfeldern des Markparenchyms grossentheils lateralwärts von den Markströngen" is somewhat confusing, for it is strictly correct only when the whole number of testes is taken into consideration. In transections of both Ligula and Schistocephalus the nerve strand was actually found to be more than half way from the median line to the margin of the medulla, but the testes were much more closely crowded in the lateral portion of the field, hence making their total number there more than in the median field. But the differences between the two fields on each side in this regard were seen in confirmatory frontal sections to be much greater in Ligula than in Schistocephalus.

LIGULA Bloch 1782

Taenia (part.)	Auctorum	
Fasciola (part.)	Linnaeus	1758
Fasciola (part.)	Linnaeus	1767
Ligula	Bloch	1782
Fasciola (part.)	Goeze	1782
Bothriocephalus (part.)	Nitzsch	1824
Ligula	Creplin	1839
Dibothrium (part.)	Donnadieu	1877

Bothria as well as external segmentation completely absent from the larvae, both develop simultaneously with the maturation of the sex-organs in the definitive host, where the external segmentation which does not correspond with the internal is confined to the anterior end. Longitudinal and transverse muscles irregularly interwoven in the anterior end, posteriorly separated into an inner transverse and an outer longitudinal layer.

Type (and only) species: *Ligula intestinalis* (L.).

LIGULA INTESTINALIS (Linnaeus 1758)
[Figs. 1, 2, 78, 98]

LARVAL STAGE:

1713	Taenia	Geoffroy	1713 : 50
1740	*Taenia capitata*	Frisch	1740 : 121
1758	*Fasciola intestinalis*	Linnaeus	1758 : 649
1767	*Fasciola intestinalis*	Linnaeus	1767 : 1078
1781	*Taenia cingulum*	Pallas	1781 : 95
1782	*Ligula piscium*	Bloch	1782 : 2
1782	*Fasciola abdominalis*	Goeze	1782 : 187
1790	*Ligula abdominalis*	Gmelin	1790 : 3043
1790	*Ligula a. alburni*	Gmelin	1790 : 3043
1790	*Ligula a. bramae*	Gmelin	1790 : 3043
1790	*Ligula a. carassii*	Gmelin	1790 : 3043
1790	*Ligula a. cobitidis*	Gmelin	1790 : 3043
1790	*Ligula a. cyprinorum*	Gmelin	1790 : 3043
1790	*Ligula a. gobionis*	Gmelin	1790 : 3043
1790	*Ligula a. leuscisci*	Gmelin	1790 : 3043
1790	*Ligula a. trincae*	Gmelin	1790 : 3043
1790	*Ligula a. vimbae*	Gmelin	1790 : 3043
1790	*Ligula petromyzontis*	Schrank	1790 : 119
1793	*Ligula salvelini*	Schrank	1793 : 143
1802	*Ligula simplicissima*	Rudolphi	1802 : 99
1803	*Ligula alburni*	Zeder	1803 : 266
1803	*Ligula bramae*	Zeder	1803 : 263
1803	*Ligula carassii*	Zeder	1803 : 262–3
1803	*Ligula cobitidis*	Zeder	1803 : 266
1803	*Liguli colymbi*	Zeder	1803 : 266
1803	*Ligula gobionis*	Zeder	1803 : 265
1803	*Ligula leucisci*	Zeder	1803 : 265
1803	*Ligula trincae*	Zeder	1803 : 265
1803	*Ligula vimbae*	Zeder	1803 : 295
1810	*Ligula acuminata*	Rudolphi	1810 : 24
1810	*Ligula cingulum*	Rudolphi	1810 : 20–22, 31
1810	*Ligula constringens*	Rudolphi	1810 : 22–24
1810	*Ligula contortrix*	Rudolphi	1810 : 18–19
1819	*Ligula simplicissima*	Rudolphi	1819 : 134
1819	*Ligula crispa*	Rudolphi	1819 : 134–135
1819	*Ligula edulis*	Briganti	1819 : 209
1839	*Ligula simplicissima*	Creplin	1839 : 295
1839	*Ligula monogramma*	Creplin	1839 : 296
1839	*Ligula digramma*	Creplin	1839 : 296
1853	*Ligula simplicissima*	Baird	1853 : 95
1855	*Ligula monogramma*	Leidy	1855 : 444
1861	*Ligula monogramma*	Van Beneden	1861 : 139
1891	*Ligula catostomi*	Linton	1891 : 66
1896	*Ligula monogramma*	Zschokke	1896 : 773, 774, 775
1898	*Dibothrium ligula*	Linton	1898 : 438
1899	*Ligula abdominalis*	Lühe	1899 : 52

ADULT STAGE:

1782	*Ligula avium*	Bloch	1782 : 4
1782	*Fasciola intestinalis*	Goeze	1782 : 183

ADULT STAGE

1790	*Ligula intestinalis*	Gmelin	1790 : 3042
1802	*Ligula simplicissima*	Rudolphi	1802 : 99
1803	*Ligula colymbi*	Zeder	1803 : 266
1810	*Ligula uniserialis*	Rudolphi	1810 : 12
1810	*Ligula alternans*	Rudolphi	1810 : 13
1810	*Ligula interrupta*	Rudolphi	1810 : 15
1810	*Ligula sparsa*	Rudolphi	1810 : 16
1819	*Ligula uniserialis*	Rudolphi	1819 : 132
1819	*Ligula alternans*	Rudolphi	1819 : 133
1819	*Ligula interrupta*	Rudolphi	1819 : 133
1819	*Ligula sparsa*	Rudolphi	1819 : 133
1824	*Bothriocephalus semiligula*	Nitzsch	1824 : 98
1839	*Ligula uniserialis*	Creplin	1839 : 296
1839	*Ligula interrupta*	Creplin	1839 : 296
1844	*Ligula sparsa*	Bellingham	1844 : 165
1845	*Ligula uniserialis*	Dujardin	1845 : 628
1845	*Ligula alternans*	Dujardin	1845 : 629
1845	*Ligula interrupta*	Dujardin	1845 : 629
1845	*Ligula sparsa*	Dujardin	1845 : 629
? 1845	*Ligula nodosa*	Dujardin	1845 : 629
1850	*Ligula monogramma*	Diesing	1850 : 579
1850	*Ligula digramma*	Diesing	1850 : 580
1853	*Ligula interrupta*	Baird	1853 : 96
1853	*Ligula sparsa*	Baird	1853 : 96
1854	*Ligula monogramma*	Diesing	1854 : 19
1854	*Ligula digramma*	Diesing	1854 : 18
? 1856	*Ligula reptans*	Leidy	1856 : 46
1863	*Ligula monogramma*	Diesing	1863 : 230
1863	*Ligula digramma*	Diesing	1863 : 231
1870	*Ligula monogramma*	Willemoes-Suhm	1870 : 94
1877	*Dibothrium ligula*	Donnadieu	1877 : 495
1881	*Ligula simplicissima*	Moniez	1881 : 37, 81
1882	*Ligula simplicissima*	Kiessling	1882
1884	*Dibothrium ligula*	Zschokke	1884 : 26
1885	*Ligula simplicissima*	Schauinsland	1885 : 550
1888	*Ligula simplicissima*	Niemiec	1888 : 2
1893	*Ligula monogramma*	Olsson	1893 : 15
1894	*Ligula simplicissima*	Stiles and Hassall	1894 : 331
1895	*Ligula monogramma*	Zernecke	1895 : 93
1895	*Ligula digramma*	Zernecke	1895 : 93
1896	*Ligula simplicissima*	Zschokke	1896 : 773, 774, 775
1898	*Ligula digramma*	Cohn	1898 : 134
1898	*Ligula uniserialis*	Lühe	1898 : 286
1898	*Ligula uniserialis*	Muehling	1898 : 32
1898	*Ligula monogramma*	Stossich	1898 : 118
1899	*Ligula intestinalis*	Lühe	1899 : 52
1900	*Ligula avium*	Braun	1900 : 1687
1900	*Ligula uniserialis*	Wolffhuegel	1900 : 63
1901	*Ligula intestinalis*	Linstow	1901a
1902	*Ligula monogramma*	Parona	1902 : 7
1902	*Ligula intestinalis*	Schneider	1902a : 13
1903	*Ligula intestinalis*	Linstow	1903 : 20
1910	*Ligula intestinalis*	Lühe	1910 : 18

Specific diagnosis: With the characters of the genus. Large worms from 100 to 1000mm. in length by 5 to 15mm. in breadth. Anterior end rounded, protruding; bothria faint. Strobila greatly elongate, depressed, maximum breadth anterior to the middle, gradually tapering to the posterior end. Body crossed by irregular ridges and furrows, and wavy at the margins in the adult, with 35 to 40 external segments anteriorly. Deep median groove on each surface in the larva, two very shallow parallel grooves near the median line on the dorsal surface in the adult.

Cuticula 5 to 20μ in thickness, subcuticula 50 to 110μ. Nerve strands 50 to 100μ in diameter. Excretory vessels numerous in three layers, one close beneath, among or just outside of the vitelline glands (cortical), another among the main body muscles, and a third in the medulla.

Genitalia from 0.05 to 0.20mm. apart. Genital cloaca a narrow transverse slit, 0.18 to 0.20 by 0.02 to 0.03mm. into which open separately the cirrus, uterus, and vagina, the latter constantly between the other two which alternate irregularly from side to side.

Testes interrupted only medially, 20 to 40 in transection, 115 to 145 by 80 to 85 by 45 to 55μ in dimensions. Vas deferens up to 35μ in diameter, loosely coiled above the cirrus-sac. Seminal vesicle small, close above the latter, 65 to 100 by 40 to 90μ. Cirrus-sac somewhat lateral, ovoid, with thin walls, 185 to 215 by 130 to 160 by 130 to 145μ. Cirrus proper within cirrus-sac, long and coiled, 25μ in diameter.

Vagina 15 to 30μ in diameter, receptaculum seminis 75 to 90μ. Spermiduct short, 20 to 25 by 6 to 12μ. Ovary 0.5 to 1.5 mm. in diameter; wing greatly depressed, isthmus prominent and not in the median line but alternating irregularly from side to side opposite the cirrus-sac; ova in same 12 to 15μ in diameter. Oocapt 18 to 20μ in diameter, oviduct 15 to 20μ. Vitelline reservoir ellipsoidal in shape, sharply separated from the duct on either side, 40 by 30μ. Vitelline follicles irregular in shape, 50 to 70 by 15 to 30μ, in a layer close beneath the subcuticula and broken only ventrally. Shell-gland composed of much elongated cells with enlarged bodies and narrow necks connecting with the oviduct for 30μ of its length. Uterus a mass of coils in the median line, 0.4 to 0.6mm. in diameter, that of the tube being 30 to 60μ.

Eggs, 50 to 65 by 30 to 42μ.

Habitat: As larvae in the body-cavities of teleosts; adults in the intestines of wading and diving birds.

HOST	LOCALITY	COLLECTOR	AUTHORITY
Larval stage:			
Leuciscus rutilis	.....	Zschokke	Zschokke 1884 : 26
Abramis brama	East Prussia	Schauinsland	Muehling 1898 : 33
Cyprinus alburnus	Berlin	Goeze	Goeze 1782 : 187
Aspius rapax	Iljmen-See, Novogorod	Varpachovskij	Linstow 1903 : 285
Gobio vulgaris	.....	Rudolphi	Diesing 1850 : 581
Carrassius gibelio	.....	Rudolphi	Diesing 1850 : 581
Petromyzon branchialis	.....	Schrank	Rudolphi 1810 : 24
Cobitis taenia	.....	Bloch	Rudolphi 1819 : 134
Salmo salvelinus	.....	Schrank	Diesing 1850 : 581
Coregonus wartmanni	.....	Schrank	Diesing 1850 : 581
Siluris glanis	.....	Mus. Vienna	Diesing 1850 : 581
Esox lucius	Sweden	Olsson	Olsson 1893 : 15
Perca fluviatilis	L. Storsjön, Jemtland, and Bönan, Sweden	Olsson	Olsson 1893 : 15
Lucioperca sandra	.....	Mus. Vienna	Diesing 1850 : 581
?Phoca vitulina	Berlin	Rudolphi	Rudolphi 1819 : 135
Morrhua americana	.....	Schafirt	Leidy 1855 : 444
Squalius cephalus	.....	Zschokke	Zschokke 1884 : 26
Alburnus lucidus	Langviken Bay, Finland	Levander	Schneider 1902a : 13
Atherina mocho	Cagliari	Parona and Mazza	Parona and Mazza 1900 : 233
Blicca bjorkna	.....	Linstow	Linstow 1901a : 629
Catostomus ardens	Yellowstone Nat. Park	D. S. Jordan	Linton 1891 : 65
Chondrostoma nasus	Basel	Zschokke	Zschokke 1896 : 775
Catostomus latipinnis	Gila R. and Salt R., Arizona	E. Palmer	Linton 1898 : 438
Osmerus mordax	Potomac R., Hagerstown, Md.	C. E. Ridenour	Linton 1898 : 438
Hybognathus nuchalis	.....	.....	Linton 1898 : 438
Notropis cornutus	Fourth Lake, Adirondacks, New York	F. Mather	Linton 1898 : 438
Schizopygopsis kozlovi	Tan-la-Gebirge, Tibet	Przevalskij	Linstow 1903 : 285
Nemachilus strauchi	Issyk-kul-See, Bai Karasu	P. Schmidt	Linstow 1903 : 285
Tinca vulgaris	.....	.....	Neveu-Lemaire 1909 : 88
Gobio gobio	.....	.....	Lühe 1910 : 19
Scardinius erythrophthalmus	.....	.....	Lühe 1910 : 19
Ameiurus sp.	Charlevoix,	H. B. Ward	Cooper (the present paper)
Alosa ohiensis	Keokuk, Iowa	H. B. Ward	"
Perca fluviatilis	Walnut Lake, Michigan	H. B. Ward	"

HOST	LOCALITY	COLLECTOR	AUTHORITY	
Perca flavescens	Go-Home Bay, Muskoka District, Ontario	A. R. Cooper	"	
Catostomus commersonii	Walnut Lake, Michigan	H. B. Ward	"	
Catostomus commersonii	Douglas Lake, Michigan	H. R. Hill	"	
Catostomus commersonii commersonii	Douglas Lake, Michigan	A. R. Cooper	"	
Notropis cornutus	Go-Home Bay	A. R. Cooper	"	
Notropis cayuga	Douglas Lake, Michigan	H. R. Hill	"	
Notropis hudsonius	Douglas Lake, Michigan	G. R. LaRue	"	
Micropterus dolomieu	Go-Home Bay	A. R. Cooper	"	
Ambloplites rupestris	Go-Home Bay	A. R. Cooper	"	
Ambloplites rupestris	Douglas Lake, Michigan	G. R. LaRue	"	
Gasterosteus bispinosus atkinsii	Chamcook Lake, New Brunswick	A. R. Cooper	"	
Ambystoma sp.	Sand Hills, Nebraska	G. R. LaRue	"	
Ambystoma tigrinum	Cherry Co., Nebraska	G. R. LaRue	"	
Free on shore	Douglas Lake, Michigan	H. R. Hill	"	
		G. R. LaRue	"	
		A. R. Cooper	"	
Adult stage:				
Falco albicilla	Greiphswald	Creplin	Creplin	1839 : 296
Ciconia alba	....	Hildebrandt	Diesing	1850 : 580
Ardea nycticorax	....	M. C. V.	Diesing	1850 : 580
Colymbus arcticus	.....	Mehlis	Diesing	1850 : 581
Podiceps auritus	Varese	Parona	Parona	1902 : 7
Anas boschas fera	.....	Mus. Vienna	Rudolphi	1819 : 134
Larus argentatus	Kainsk, Enissej	Middendorff	Linstow	1903 : 20
Sterna hirundo	.....	Mus. Vienna	Rudolphi	1819 : 133
Mergus serrator	Gulf of Finland	Schneider	Schneider	1902a : 13
Nycticorax nycticorax	.....	.....	Lühe	1910 : 18
Graculus carbo	.....	M. Siebold, Coll. Brit. Museum	Baird	1853 : 96
Fuligula clangula	Jemtland	Olsson	Olsson	1893 : 15
Xema minutum	Trieste	Stossich	Stossich	1898 : 118
Urinator arcticus	....	.....	Lühe	1900 : 18
Rissa tridactyla	.....	.....	Lühe	1900 : 18
Stercorarius parasitica	.....	.....	Lühe	1900 : 18
Hydrochelidon nigra	.....	.....	Lühe	1910 : 18
Herodias alba	....	.....	Lühe	1910 : 18
Haliaetus albicilla	.....	.....	Lühe	1910 : 18

HOST	LOCALITY	COLLECTOR	AUTHORITY
Aquila chrysaetus			Lühe 1910 · 18
Corvus cornix			Lühe 1910 18
Podilymbus podiceps		H. B. Ward	Cooper (the present paper)
Merganser sp.	Urbana, Illinois	H. B. Ward	"
Colymbus hoelbeelli		H. B. Ward	"
Mergus merganser	Douglas Lake, Michigan	G. R. LaRue	"

The species has also been reported in Europe and Asia from the following additional hosts:

Larval stages: *Abramis bjorkna, A. blicca, A. vimba, Alburnus alburnus, Ammocoetes branchialis, Aspius alburnus, Carassius carassius, C. vulgaris, Cobitis aculeata, Cyprinus blicca, C. brama, C. carassius, C. gobio, C. lacustris, C. leuciscus, C. tinca, Gobio fluviatilis, Leuciscus erythrophthalmus, L. leuciscus, L. phoxinus, L. pulchellus, L. vulgaris, Lucioperca lucioperca, Squalius turcicus.*

Adult stages: *Ardea alba, A. ciconia, A. egretta, Ciconia ciconia, C. nigra, Colymbus auritus, C. cristatus, C. griseigena, C. rubricollis, C. septentrionalis, C. subcristatus, Falco chrysaetos, F. fulvus, Larus canus, L. melanocephalus, L. parasiticus, L. pelecanus carbonis, L. pygmaei, L. ridibundus, L. tridactylus, Mergus albellus, M. merganser, M. minutus, Podiceps minor, P. nigricollis, P. rubricollis, Sterna nigra, Totanus chloropus, Urinator stellatus, Xema ridiundum.*

As indicated in the above synonymy, the greatest confusion has existed in connection with this species from the time of Linnaeus to that of Lühe (1899), all of the older writers recognizing at least two species, the larval and the adult, and many, several species under each of these. Rudolphi (1810), for instance, accepted four species of the former, "ovariis occultatis," and the same number of the latter, parasitic in the intestines of birds, "ovariis distinctis." In his Entozoorum Synopsis (1819) he reduced the number of larval species to two, but retained the same four adult forms as before. The next important move in a systematic direction was by Creplin (1839) who divided Rudolphi's *L. simplicissima* into two larval species, viz., *L. monogramma* and *L. digramma*, corresponding respectively to the previously known *L. uniserialis* and *L. interrupta* (or *alternans*), which plan was followed by Diesing (1850, 1854, and 1863) while Dujardin (1845) and Baird (1853) followed Rudolphi. Diesing (1850:581) erected a third species, *L. reptans*, to accommodate numerous forms found encysted in the muscles and connective tissues of amphibians, reptiles, birds and mammals; but as pointed out by Janicki (1906:519) several larval species were probably included under this heading. Those from avian hosts are not given above since they were found only among the

muscles and under the skin, where *L. intestinalis* has never been found in birds, so far as the available records indicate. Lühe (1910:18) did not include them in his list of hosts for the adult stage of the species.

Next in order of importance came Donnadieu's (1877) classical experiments in which, after completely reviewing the literature up to date, he conclusively proved that the form found in the body cavities of various bony fishes is the larval stage of that present in the intestines of birds. As a result of his work he combined the two forms under a new name, *Dibothrium ligula*, confusing at the same time *Schistocephalus solidus* with *Ligula intestinalis*. The life-history of the species was later studied by Riehm (1882) by feeding methods. Moniez (1881:37, 81) was the first writer to study the histology of the species, while Kiessling (1882) gave the first description of its general anatomy. As emphasized, however, by Linstow (1901a), Kiessling's work is not very specific, since he almost constantly disposed of *L. intestinalis* by saying that in it conditions were the same as in *Schistocephalus solidus*. While, apart from Donnadieu and the earlier writers, Willemoes-Suhm (1870:94) was the first to study the development of the embryo with attention to detail, Schauinsland (1885:550) enlarged upon his observations and gave a more or less complete description of the process up to the time of the escape of the ciliated larva. Niemiec (1888:2) described the nervous system, and Cohn (1898:134) pointed out its resemblance to *Sch. solidus* in this regard. Zernecke (1895) in the meantime dealt in his well known work on the finer structure of cestodes with the parenchyma and the nervous and muscular systems in particular; since then little has been done in that connection. The question of segmentation was studied by Lühe (1898). Later the same writer (1899:52) placed the species in his first classification, stating as his belief that there is only one species of Ligula, viz., *L. intestinalis* (L). The latter conclusion was also arrived at by Linstow (1901a:628), altho he attributed the specific name to Goeze; while in his latest classification Lühe (1910) maintained the same view.

Consequently, taking for granted in the absence of European material for comparison that the latter has been established as a fact for the European forms, the problem is to determine whether the same species occurs here in America. So far as the majority of specific characters are concerned, one must rely on the descriptions of Kiessling and Linstow (1901a) who seem to have been the only writers to attend to the details of the reproductive system,—and as metioned above, Kiessling's is quite inadequate in this connection. The only American reports of the species are of larval forms: *L. monogramma* by Leidy (1855:444) and *Dibothrium ligula* by Linton (1898:438), the former having also listed (1856:46) the doubtful *L. reptans*.

Lühe (1910:18) gave the dimesions of the species as 100 to 400 mm. (occasionally 1 meter) in length by from 5 to 15mm. in breadth, not distinguishing however, between the larva and the adult in this regard. Linstow (1901:629) reported a larva from *Blicca bjorkna* 200mm. long, 9 broad and 3.5 thick, adults from *Podiceps cristatus* and *Merganser merganser* 160mm. long, 4 broad and 1.5 thick. Concerning these differences he said that: "Wenn man die Geschlechts-

form aus Vögeln oft kleiner findet als die Larve aus Fischen, so mag das seinen Grund darin haben, dass die letztere sich in der Grösse ihren Wirth anpasst; die grossen Larven in grossen Fischen können aber nicht von kleineren Vögeln verschlungen werden." The largest larval specimen at hand was one from *Catostomus commersonii* which measured 425mm. in length by 15 in maximum breadth, but the largest adult from *Merganser merganser* was only 217 by 6mm. In the larva the anterior end is somewhat bluntly rounded (Fig. 1), the bothria being visible as very short grooves passing over the tip, while in the adult they are more elongated and distinct, the end of the strobila being somewhat protruded as shown in figure 2. On each surface of the larva there is a deep, median, longitudinal furrow, which however, becomes obliterated in the adult, excepting anteriorly, by the growth of the reproductive organs, the ducts of which are confined to the median line of the strobila. When these are developed the strobila is characterized dorsally by a low median ridge bounded on each side by a quite shallow groove, and ventrally by a greater thickening of the median line, not separated, however, by any grooves from the lateral regions. The whole strobila gradually tapers from a short distance behind the anterior end, where the maximum breadth is located, to the posterior end. Whereas in the larva it is quite thick, in the adult it is thin and leaf-like, the margins usually appearing wavy in alcoholic specimens, especially posteriorly. A pseudosegmentation is present in the anterior end of the strobila, but as has been known, especially since Lühe (1898) emphasized the fact, this division of the strobila into segments does not correspond with the internal division into true proglottides. Gemmill (1909:11) counted about 50 of them in the anterior third of the worm, the writer 38 or 39 for a distance of 13mm. from the tip of one adult specimen (Fig. 2) and 36 for 10mm. in another. They vary considerably in length and are often incomplete medially. From the anterior region showing external segmentation to the posterior end both larvae and adults, but particularly the latter, are crossed by very numerous irregular grooves, which give the worm its characteristic appearance apart from the general shape as contrasted, for instance, with the closely related *Schistocephalus solidus*. The smallest larva met with was one from a small specimen of *Micropterus dolomieu*, 47mm. in length. It gave the following measurements: length, 4.9mm.; maximum width, 0.54mm.; width one-third the length from the anterior end, 0.54mm., two-thirds, 0.37mm.; length of bothrial groove about 0.07mm.

The cuticula was found to have a thickness of from 5 to 15μ, compared with 16 to 18μ by Kiessling and 2.1 (!) by Linstow. It appears homogeneous in sections rather than divisible into the three layers described by the former, with some tendency, however, for the outer one-quarter to one-sixth to take the stain much less than the remainder of the tissue, which outer clearer area is often bounded by a very delicate pseudociliated layer. There is a good deal of variation not only in the thickness of the cuticula but also in its structure; and these remarks apply to the larva as well as to the adult. The subcuticula varies from 50 to 110μ in thickness, or 33 to 49μ according to Kiessling and

114μ to Linstow. Calcareous bodies in the characteristically fine parenchyma, described by Moniez and Zernecke, and given dimensions of 13 by 7.8μ by Linstow, were observed in the largest living specimens from the body-cavity of *Catostomus commersonii commersonii* to be extremely numerous, spherical to ellipsoidal in shape and to measure from 14 to 19μ in length by 12 to 17 in breadth.

The musculature has been well described histologically by Zernecke (1895); while Kiessling spoke rather briefly of its arrangement in the late larva. Later Lühe dealt with the system in general (1897a and 1898) and its relation to the nervous system (1896), and Linstow (1901a), gave a concise account of its arrangement.

The chief nerve strands are situated in transections between the lateral and median quarters of the transverse diameter of the strobila, in the median frontal plane, that is below the neighboring testes, and with a diameter of 50 to 100μ. The details of the system have been studied by Moniez (1881), Niemiec (1888), Zernecke (1895), and Cohn (1898), the latter of whom found conditions pretty much as in Schistocephalus, namely, that each chief strand has associated with it six collateral strands, arranged in three groups of two each.

The excretory system was studied by Moniez and Zernecke in considerable detail. Linstow stated that two regions accommodating numerous longitudinal vessels are present: (1) an outer, close beneath the vitelline glands, and (2) an inner, between the inner longitudinal and transverse muscles, or as Linstow figured, between the former themselves. In the material studied an outer plexus appeared close beneath, among, or most often just outside of the vitelline glands (cortical); a second and quite indistinct one among both sets of muscles, and a third, or innermost layer, as prominent as the outermost, almost in the median frontal plane of the medulla.

The sets of genitalia, beginning about 10mm. from the anterior end and very closely crowded together in the longitudinal direction, lie from 0.05 to 0.20mm. apart, 0.13 to 0.15mm. being the data given by Linstow. The openings are usually almost exactly in a transverse line; but the cirrus and uterus openings alternate irregularly from side to side, that of the vagina being constantly in the middle. This alternation of the openings is due to the similar alternation of the internal organs and evidently was the basis upon which the earlier species *L. digramma* and *L. alternans* were established. The genital cloaca is a quite irregular transverse depression, 0.18 to 0.20mm. in width and 0.02 to 0.03mm. in length, the respective measurements by Linstow being 0.106 and 0.026mm.

"The testes lie in a single row, which is only interrupted by the uterus, on the dorsal side of the medulla. . . ." They are from 20 to 40 in number in transections, ellipsoidal in shape, their greatest diameters being transverse, as indicated by the maximum width, length, and depth being, respectively, 115 to 145, 45 to 55, and 80 to 85μ. Linstow gave them as 150 to 180μ long by 88 to 156μ wide. The loosely coiled vas deferens is situated above the cirrus-sac

(Fig. 78) and roughly divided into two parts by the lateral coils of the uterus, one part being immediately above the cirrus-sac and the other close to the dorsal body wall. The duct attains a diameter of 35μ when filled with spermatozoa. Distally it expands into the very small (as compared to that of *Sch. solidus*) seminal vesicle, situated close to the dorsal wall of the cirrus-sac. The vesicle is from 65 to 100μ in length by 40 to 90μ in diameter (156 by 86μ, Linstow), oval in shape, the narrower end towards the cirrus pouch, and provided with only a comparatively feeble musculature. The wall of the structure is richly supplied both internally and externally with nuclei which are respectively those of the lining epithelium and the myoblasts, as in Schistocephalus. The epithelium is strongly ciliated. The cirrus-sac (Fig. 78) is an ovoid body, somewhat flattened dorso-ventrally and obliquely by the uterus, and alternating irregularly from right to left, always occupying the opposite side of the median line from the ovarian isthmus and the neighboring female ducts. Its wall is quite thin, while apart from the cirrus proper which occupies the distal two-thirds, the contents consist of loose parenchyma and only a few retractor muscles. The measurements of the organ in sections are: dorsoventral diameter, 185 to 215; width, 130 to 160; and length, 130 to 145μ; which are quite at variance with Linstow's diameter of 53μ of what he described as a spherical organ. Within the cirrus-sac the vas deferens is not sharply separated into ejaculatory duct and cirrus proper, altho the latter is quite distinct, closely coiled, and as much as 25μ in diameter.

The vagina opens into the common genital cloaca, if one may use that name for the depression mentioned above, in the median line and usually equidistant from the openings of the cirrus and uterus. It passes dorsally thru the cortex and the musculature with almost a straight course. Then within the medulla it turns sharply posterolaterally, in which portion of its course it has a diameter of from 15 to 30μ (5μ, Linstow). Its thin lining of cuticula, directly continuous with that of the genital depression, gradually passes into a nucleated epithelium, in which no distinct cell boundaries appear, just within the cortex. Dorsal to the ovarian isthmus it enlarges into an elongated receptaculum seminis which has a diameter of from 75 to 90μ. Linstow described a spindle-shaped terminal receptacle, 13μ in diameter, and an oocapt as follows: "dorsal von der Vereinigungsstelle der beiden Keimstocksflügel liegt der ovale, 0.088mm. lange und 0.066mm. breite Schluckapparat"; each of which, however, in comparison with that described here by the writer and for *Sch. solidus* below, seems to have been confused with the other. At least the oocapt of none of the bothriocephalids described here is relatively so large as indicated by Linstow in his measurements and in his figure, nor is the receptaculum as spindle-shaped as shown in the latter. In this connection Kiessling described a swelling of the vagina, 46μ in diameter, which contained spermatozoa. The spermiduct is so short and of such a small calibre that it is quite difficult to locate it in sections. After pursuing a horizontal course it unites with the oviduct a short distance from the oocapt (Fig. 98) much as in *Sch. solidus*. It is from 20 to 25μ in length and 6 to 12μ in diameter. The ovary is asymmetrical, as stated by Kiessling but

denied by Linstow, since it consists of a much depressed lateral wing, situated close to the ventral musculature (Fig. 78) and a more median enlarged portion which functions as the isthmus in that the oviduct arises from it. This isthmus-like region is not in the median line but about 0.25mm. from it, the whole organ alternating irregularly from right to left, constantly opposing the cirrus-sac on the other side. It varies from 0.55 to 0.64 mm. in width and has a length laterally of 0.12mm. Its unusual situation is evidently due to the closely crowded condition of the reproductive organs and the pressure exerted by the large uterus in the median line. Whereas the wing has a maximum dorsoventral diameter of about 60μ, the isthmus is about 95μ in depth and roughly ellipsoidal in shape, protruding in sections from the dorsal region of the junction of the wing (Fig. 78). Ova from the isthmus were found to be oval to spherical in shape and from 12 to 15μ in diameter (13 to 16μ, Linstow). The oocapt is directed horizontally away from the side of the isthmus and from the median line. Its diameter is from 18 to 20μ,—with which compare the dimensions of 88 by 66μ given by Linstow. The oviduct has a diameter of from 15 to 20μ. Taking a general dorsal course, after being joined by the spermiduct, it soon receives the common vitelline duct (Fig. 98) which has only a limited enlargement from a previous diameter of 10 to 20 to 30μ in the form of a vitelline reservoir, located close to the oviduct with a length of 40μ. The vitelline follicles are situated in a layer close beneath the subcuticula and unbroken, excepting in the median ventral line. The individual follicles, very irregular in shape, are 50 to 70μ in depth and 15 to 30μ in width, Linstow's measurements being 65 by 47μ and Kiessling's 6μ in the larva. Concerning the shell-gland Linstow said: "Die Schalendrüse ist ein 0.088-0.105mm. grosses Organ, das dorsal von der Mitte des einen Keimstockflügels an der entsprechenden Aussenwand der Uterus liegt; die Zellen, deren kleiner Kern sich intensiv farbt, sind 0.0039mm. gross." In the sections studied by the writer it was found to be a quite irregular structure, composed of greatly elongated club-shaped cells with necks of different lengths which unite with the oviduct in a region only about 30μ in length and situated just beyond the point of reception of the common vitelline duct (Fig. 98). These cells are so loosely arranged and their proximal attenuated portions of such a filiform nature that they are very easily overlooked, especially since they are scattered thruout the whole of the dorsoventral diameter of the medulla of the region and are interwoven among the oviduct, the receptaculum, the vitelline duct and the beginning of the uterus. They form by no means such a compact organ as Linstow's description and figure would indicate. The distal ends of the cells are about 15 by 10μ in size, while their nuclei are about 4μ in diameter. Kiessling described the shell-gland as similar to that of *Sch. solidus*, and as follows: "Die Schalendrüse besteht aus Drüsenzellen, welche an feinen Stielchen befindliche Bläschen an der Oberfläche einer Halbkugel angeordnet sind und ihre Stielchen als Radien nach dem Mittelpunkte der Kugel senden." His figures of such a compact region are likewise quite different from conditions described here. The uterus forms a mass of coils, 0.4 to 0.6mm. in diameter in the median

line, from which a straight portion passes ventrally thru the musculature and cortex to the opening which is about 20μ in diameter (35μ, Linstow). The diameter of the duct is 60μ in the median frontal plane but only half that amount as it passes thru the longitudinal muscles. The measurements of the eggs are according to Kiessling and Linstow, respectively, 49 by 34μ and 65 by 42μ: they were found by the writer to be 50 to 54 by 30 to 33μ in sections.

Our knowledge of the life-history of the species is confined chiefly to the works of Duchamp (1876), Donnadieu (1877) and Riehm (1882) who firmly established the well-known fact that the larva present in the abdominal cavities of various species of teleosts develops rapidly in the intestines of fish-eating birds. The production of eggs begins after about 36 hours, while the adults live for from three to four days only in the definitive hosts. Apart, however, from these and other closely related details which were brought out by Donnadieu by means of well conducted and controlled experiments, nothing is known, so far as the writer is aware, of the development of the oncosphere in the intermediate host up to the time when it becomes distinguishable as a small larva. The measurements of the smallest larva found in connection with this study have been given above; another slightly larger specimen was 6.1mm. in length by 1.34mm. maximum breadth.

Altho the above description shows many discrepancies between the species as here dealt with and the European form, the writer does not feel justified in separating the two specifically, especially in the absence of European material for comparison. The thickness of the cuticula, and subcuticula, the dimensions of the testes, seminal vesicle and cirrus-sac and the diameter of the vagina show the greatest differences, apart from the probable confusion by Linstow of the oocapt and receptaculum seminis, while the measurements of the eggs as here given are somewhat intermediate between those by Kiessling and Linstow. But the fact that the data given by the latter are apparently the only adequate ones for the adult and that there are not a few discrepancies between Kiessling's and Linstow's accounts restrains one from looking upon this, the American form, as new. In dealing with this question of identity it must also be remembered that not only does the species vary so much that, as pointed out above, a great deal of confusion exists in the earlier literature, but that the number of host species of the larva as well as of the adult is very large as compared to other species of bothriocephalids, hence introducing greater factors for variation. And above all the geographical distribution of the wading and diving birds harboring the mature worms is such that here in America there are many of the same species as well as the same genera that occur in Europe. As the above record of hosts indicates, the species certainly ranges widely over Europe and Northern Asia, so that it would be quite surprising if it did not occur here in North America, with the probable region of transition in Iceland and Greenland on the east and northeastern Siberia and Alaska on the west. However apart from Leidy's and Linton's records it has apparently not been reported up to the present.

The material studied by the writer consisted of the following lot of larvae: Nos. 4706 and 4708 of the collection of the United States National Museum; Ch 18a, 16.411, 16.413, 16.414, 16.419, 17.31 and 17.32 of the collection of the University of Illinois, under the care of Professor H. B. Ward; Nos. 49b, 70 to 79, 110 to 119, 361 to 370, 427 and 431c of the collection of Dr. G. R. LaRue; Nos. II, III, IV, and V from the collection of Mr. H. R. Hill; and Nos. 47, 54, 150, 158, 159, 160, 189, 190, 312, 313, 314, 317, 319, and 330 of the writer's collection; and the adults contained in Nos. La 156, 17.184, and 17.185 of the collection of the University of Illinois, respectively from the intestines of *Merganser* sp., *Podilymbus podiceps* and *Colymbus holboellii*, and No. 387g of the collection of Dr. LaRue from the intestine of *Mergus merganser*.

SCHISTOCEPHALUS Creplin 1829

Taenia (part.)	Auctorum	
Hirudo (part.)	Linnaeus	1745
Fasciola (part.)	Linnaeus	1767
Rhytis (part.)	Zeder	1800
Halysis (part.)	Zeder	1800
Bothriocephalus (part.)	Rudolphi	1808
Schistocephalus (part.)	Creplin	1829

Bothria and external segmentation developed in the larva. The tip of the scolex retractile. Segmentation complete and corresponding to the internal structure of the animal. Longitudinal and transverse muscles arranged in several alternating layers (three transverse layers enclosing two longitudinal layers).

Type (and only) species: *Schistocephalus solidus* (O. F. Müller).

SCHISTOCEPHALUS SOLIDUS (O. F. Müller 1776)

[Figs. 3, 79, 80]

LARVAL STAGE:

1734	Taenia	Frisch	1734 : 395
1745	*Hirudo depressa alba*	Linnaeus	1745 : 250
1758	*Fasciola hepatica*	Linnaeus	1758 : 648
1761	*Taenia lata*	Pallas	1761 : 410
1767	*Fasciola hepatica*	Linnaeus	1767 : 1077
1776	*Taenia solida*	Müller	1776 : 219
1780	*Taenia gasterostei*	Müller	1780 : 22
1780	*Taenia gasterostei*	Fabricius	1780 : 320
1781	*Taenia acutissima*	Pallas	1781 : 76, 78
1786	*Taenia gasterostei*	Batsch	1786 : 224
1788	*Taenia solida*	Schrank	1788 : 49
1790	*Taenia solida*	Gmelin	1790 : 3079
1790	*Taenia gasterostei*	Abildgaard	1790 : 49–58
1800	*Rhytis solida*	Zeder	1800 : 297
1810	*Bothriocephalus solidus*	Rudolphi	1810 : 57
1819	*Bothriocephalus solidus*	Rudolphi	1819 : 139, 477
1819	*Bothriocephalus solidus*	Leuckart	1819 : 46

1824	*Bothriocephalus solidus*	Nitzsch	1824 : 97
1829	*Bothriocephalus solidus*	Baer	1829 : 388
? 1863	*Schistocephalus rhynchichthydis*	Diesing	1863 : 233
1896	*Schistocephalus dimorphus*	Zschokke	1896 : 773
1896	*Schistorhynchus dimorphus*	Zschokke	1896 : 776
1898	*Schistocephalus dimorphus*	Linton	1898 : 427
1898	*Schistocephalus solidus*	Cohn	1898 : 126
1898	*Schistocephalus solidus*	Mühling	1898 : 33
1899	*Schistocephalus solidus*	Lühe	1899 : 52
1909	*Schistocephalus solidus*	Scott	1909 : 80

ADULT STAGE:

1782	*Taenia lanceolata nodosa*	Bloch	1782 ? 10
1786	*Taenia lanceolata var. β*	Batsch	1786 : 167
1788	*Taenia nodularis*	Schrank	1788 : 39
1790	*Taenia lanceolata nodosa*	Gmelin	1790 : 3075
1790	*Taenia gasterostei*	Abildgaard	1790 : 49–58
1793	*Taenia lanceolata nodosa*	Rudolphi	1793 : 41
1800	*Halysis lanceolato nodosa*	Zeder	1800 : 340
1810	*Bothriocephalus nodosus*	Rudolphi	1810 : 54
1819	*Bothriocephalus nodosus*	Rudolphi	1819 : 140
1819	*Bothriocephalus nodosus*	Leuckart	1819 : 58
1824	*Bothriocephalus nodosus*	Nitzsch	1824 : 97
1829	*Schistocephalus dimorphus*	Creplin	1829 : 95
1839	*Schistocephalus dimorphus*	Creplin	1839 : 296
1845	*Schistocephalus dimorphus*	Dujardin	1845 : 622
1850	*Schistocephalus dimorphus*	Diesing	1850 : 584
1853	*Schistocephalus dimorphus*	Baird	1853 : 92
1854	*Schistocephalus dimorphus*	Diesing	1854 : 19
1858	*Schistocephalus solidus*	R. Leuckart	1858 : 129
1859	*Schistocephalus solidus*	Steenstrup	1859 : 475
1863	*Schistocephalus dimorphus*	Diesing	1863 : 232
1869	*Schistocephalus dimorphus*	Willemoes-Suhm	1869 : 469
1877	*Dibothrium ligula*	Donnadieu	1877 : 495
1881	*Schistocephalus dimorphus*	Monniez	1881 : 175
1882	*Schistocephalus dimorphus*	Kiessling	1882
1889	*Schistocephalus solidus*	Lönnberg	1889 : 40
1890	*Schistocephalus dimorphus*	Lönnberg	1890 : 18
1893	*Schistocephalus dimorphus*	Olsson	1893 : 15
1896	*Schistocephalus dimorphus*	Ariola	1896 : 280
1896	*Bothriocephalus zschokkei*	Fuhrmann	1896
1898	*Schistocephalus zschokkei*	Fuhrmann	1898 : 144
1898	*Schistocephalus solidus*	Mühling	1898 : 33
1899	*Schistocephalus nodosus*	Lühe	1899 : 52
1900	*Schistocephalus dimorphus*	Ariola	1900 : 426
1910	*Schistocephalus gasterostei*	Lühe	1910 : 19
1911	*Schistocephalus dimorphus*	Solowiow	1911 : 123

Specific diagnosis: With the characters of the genus. Medium sized worms, length 30 to 300mm., breadth 3 to 9mm. First segment or "scolex" 0.4 to 0.8mm. in length and 1 to 1.3mm. in width. Strobila ovate-lanceolate and depressed, maximum breadth anterior to the middle; hindermost segments narrower and

flatter, 0.25 to 1.0mm. in length by 1 to 3mm. in width, forming an appendage up to 10mm. in length; medium segments 0.1 to 0.5mm. long, posterior borders prominent. Shallow median groove on the ventral surface.

Cuticula 15 to 20μ in thickness; subcuticula 40 to 65μ. Layer of internal longitudinal muscles 15 to 50μ in thickness. Nerve strands 30 to 75μ in diameter. 25 to 30 excretory vessels in transections.

Genital cloaca median, shallow, with a diameter of 90μ; no hermaphroditic duct. Opening of vagina close behind that of cirrus and to one side but not so far as that of the uterus, both alternating irregularly from side to side.

Testes extend from the median genital ducts laterally to the edges of the medulla, unbroken from proglottis to proglottis, closely crowded, 240 to 480 in number for each proglottis, 85 to 100μ in depth, 40 to 65 in width and 55 to 85 in length. Vas deferens median, dorsal, closely applied to the seminal vesicle, the whole mass 0.30mm. in diameter, the duct itself 35 to 60μ. Seminal vesicle 175 by 150μ, walls 25μ in thickness. Cirrus-sac oval in shape, immediately below the seminal vesicle, 0.185 to 0.203 by 0.203 to 0.212 by 0.166 to 0.185 mm. in dimensions. No inner seminal vesicle. Cirrus proper not sharply separated from the ductus ejaculatorius; whole surrounded by numerous retractor muscles.

Vagina 45 to 60μ in diameter just within the medulla. Receptaculum seminis large, 92 to 105μ in diameter. Spermiduct unites with the oviduct close to the ventral wall of the medulla. Ovary with large wings consisting of closely arranged tubules, whole organ 0.6mm. in width, wings 0.10 in length. Ova 13μ in diameter, their nuclei 5μ. Oocapt 35 to 40μ in diameter, oviduct 25 to 30μ. Vitelline gland unbroken at margins of the proglottis, from proglottis to proglottis, and medially, excepting for small areas above and below the proximal reproductive ducts; individual follicles 55 to 90 by 18 to 26μ. Ootype 16 to 20μ in diameter. Shell-gland slightly to one side of median line. Uterus 85 to 135μ in diameter at its middle; the terminal portion directed dorsoventrally and lined with cuticula distally; opening at the bottom of a slight invagination of the ventral body wall, formed by the rupture of a pre-existing cuticular membrane.

Eggs, 38 to 65 by 22 to 38μ.

Habitat: As larvae in the body-cavities and occasionally in the stomach and intestine of bony fishes; adults in the intestines of wading and diving birds.

HOST	LOCALITY	COLLECTOR	AUTHORITY
Larval stage:			
Gasterosteus aculeatus	Greenland	Fabricius	Fabricius 1780 : 320
Cottus poecilopus	L. Storsjön, Sweden	Olsson	Olsson 1893 : 15
Cottus bairdii	Swan R., Mont.	Everman	Linton 1898 : 427
Salmo salar	Basel	Zschokke	Zschokke 1896 : 776
Phoca vitulina	Gryphswald	Rudolphi	Rudolphi 1819 : 140
Rhynchichthys gronovii	Hayti	Weinland	Diesing 1850 : 585
Gasterosteus bispinosus atkinsii	Chamcook L., New Brunswick	A. R. Cooper	Cooper (the present paper)
Uranidea formosa	Port Credit, Ontario	A. R. Cooper	" "
Gasteroseus cataphractus	R. P. Lake, St. Paul Id., Pribilof Ids., Alaska	C. E. Crompton	" "
Adult stage:			
Corvus cornix	East Prussia	Braun	Muehling 1898 : 34
Recurvirostra avocetta	....	Schilling	Diesing 1850 : 584
Ardea stellaris	Genf	Fuhrmann	Fuhrmann 1896 : 546
Ciconia alba	East Prussia	Braun	Muehling 1898 : 34
Sterna hirundo	Gryphswald	Rudolphi	Rudolphi 1819 : 140
Colymbus septentrionalis	Firenze, Italy	Condorelli	Parona 1899 : 8
Podiceps nigricollis	Bracciano, Italy	Parona	Parona 1899 : 8
Larus ridibundus	Rossitten	Muehling	Muehling 1898 : 34
Anas glacialis	....	Creplin	Diesing 1850 : 585
Mergus serrator	L. Storsjön, Jemtland, Sweden	Olsson	Olsson 1893 : 15
Uria troile	....	Abildgaard	Diesing 1850 : 585
Alca torda	Leipzig	C. W. Stiles	Stiles and Hassall 1894 : 322
Totanus calidrus	Jaederen, Norway	Loennberg	Loennberg 1890 : 18
Harelda glacialis	Pillau	Muehling	Muehling 1898 : 34
Fuligula marila	Pillau	Muehling	Muehling 1898 : 34
Haematopus ostrealegus	Pillau	Muehling	Muehling 1898 : 34
Fulica atra	Portoferrajo, Id. Elba	Damiani	Parona 1899 : 7
Puffinus kuhli	Portoferrajo, Id. Elba	Damiani	Parona 1899 : 7
Urinator arcticus	....	....	Lühe 1910 : 19
Stercorarius parasiticus	.....	.....	Lühe 1910 : 19
Nyroca marila	.....	.....	Lühe 1910 : 19
Lophodytes cucullatus	Lincoln, Nebr.	H. B. Ward	Cooper (the present paper)

The species has also been reported in Europe from the following additional hosts:

Larval stage: *Cottus scorpio*, *Fulica atra*, *Gasterosteus pungitius*, *Totanus calidrus*, and *Rana esculenta*;

Adult stage: *Alca pica, Ardea cinerea, Ciconia ciconia, C. nigra, Colymbus arcticus, C. cristatus, C. glacialis, C. griseigena, C. immer, C. troile, Corvus corax, Larus argentatus, L. capistranus, L. marinus, Mergus albellus, Mergus merganser, Podiceps cristatus, P. rubricollis, Sterna arctica, S. macroura, S. minuta, S. nigra* and *Uria grylle.*

As indicated in the above synonymy this species was known for almost a century, at first as the larval form only and then as both larval and adult forms, before it was discovered that the two species recognized from the time of Bloch (1782) were one and the same. Abildgaard (1790), who called the worm *T. gasterostei*, seems to have been the first to consider the larval form found chiefly in sticklebacks to be the same as that found in fish-eating birds, since on feeding sticklebacks infected with the larvae to geese he obtained the adult form from the intestines of the latter. Yet Rudolphi (1810) did not agree with his conclusions but still considered that there were two distinct species, namely, *Bothriocephalus nodosus* (adult) and *B. solidus* (larva). And this continued until Creplin (1829) united both in one species under a new genus, *Schistocephalus dimorphus*. Diesing (1863:233) made a new species out of the *Schistocephalus* found by Weinland (1859) in the island of Hayti in *Rhynchichthys gronovii*, but later writers have considered that in all probability it was only the well known larval form of this species. Willemoes-Suhm (1869) was evidently the first to study the development of the fertilized ovum, which was later gone into more thoroughly by Schauinsland (1885:555). Donnadieu (1877), to whom all go back in their considerations of the larval development of Ligula, unfortunately fell into the error of considering Schistocephalus and Ligula to be not only the same specifically but generically. The anatomy was first studied by Moniez (1881:175), more thoroughly by Kiessling (1882), and still later by Furhmann (1896) (under *B. zschokkei* sp. nov.) and Solowiow (1911). Linton (1897:427) is the only one, apart from Weinland's record which is only a brief foot note, who has reported the species from America.

As regards the correct name of the species, it should be noted that, altho Lühe (1899:52) called the "typical and only species" of the genus *Sch. nodosus* (Rud.) and the larval stage *Sch. solidus* (O. F. Müller), he reverted in 1910 to "*Schist. gasterostei (Fabr.)* (=*Sch. dimorphus Crepl.*)" without, however, discussing the change. But according to the Rules of Nomenclature, Art. 27 (b), the earliest name of the larval stage must hold, so that, since Lühe himself considered this to be *Sch. solidus* (O. F. Müller), the writer makes use of the latter in the present paper.

According to Lühe (1910:19) *Sch. solidus* ranges in length from 30 to 300mm. while the maximum breadth varies from about 3 to 9mm. and is located ahead of the middle of the strobila. As shown in the table below the largest and only sexually mature specimen of the six studied by the writer was only 29mm. in length by 6mm. in breadth. The scolex (Fig. 3) is, as indicated in the above diagnosis of the subfamily, not separated from the first segment into which it runs insensibly, the whole "head" being thus triangular in shape. The bothria

are merely short median grooves which unite at the very tip not only with each other but with a frontal median groove which passes laterally into slight emarginations of the edges of the segments. While these emarginations were seen to be present in the anterior segment, gradually disappearing towards the middle of the worm, no such "flat leaflike flaps (bothria) on the lateral margins separated from each other on flat surface by a broad, shallow sulcus," as described by Linton (1898:428) and shown in his Fig. 4, Pl. XXVIII, for the first segment were met with; but the posterior border was quite entire, altho as seen in figure 3, not very prominent in the vicinity of the median line in adults as well as in larvae. The bothria of the mature specimen (H. 7 of the table below) were not present, but the region where they would otherwise be was quite smooth, only a shallow, median, frontal groove appearing. The whole strobila is ovate-lanceolate, considerably depressed and provided in the adult with a very shallow median groove on the dorsal surface (Fig. 80) which seems to be due to the slight protrusion of the median reproductive organs, chiefly the cirrus-sacs and seminal vesicles, towards the ventral surface (Fig. 79) and the consequent dragging downward of the dorsal median tissues. Concerning this matter Linton said "*S. dimorphus* is described as having in the larval state a longitudinal median furrow on each face. These specimens do not exhibit this character; neither do they have anything that can be properly called a costa dividing the two bothria." While in the specimens studied the dorsal groove was present not only in the adult but (not so well marked) in the larva, a similar ventral groove was also noticed in sections of the anterior end of one of the latter. Both grooves, however, are in either case so shallow as to be easily overlooked in alcoholic specimens; they seem to be of only secondary importance since they are apparently quite variable in their nature. While the segments in the anterior region of the strobila are very broad and comparatively thick, short, and from 0.1 to 0.5mm. in length, posteriorly the strobila is considerably smaller and flatter, especially in mature individuals. In larvae the segments are much more irregular in outline and as much as 1mm. long (0.75 in the only ripe specimen studied). The segmented condition of the strobila, in contrast with that of Ligula, is rendered more apparent by the prominent posterior borders of the anterior and middle proglottides which at the margins produce the characteristic saw-tooth effect. The following table gives the measurements of two specimens with those by Linton for comparison:

NUMBER	72	H 7	4727 U. S. N. M.
Length	17mm.	29mm.	32mm.
Maximum breadth	5.5	6	6
Length of "cauda"	1.64	10	?
Breadth of same	1.1	2-3	2.5
Length of med. segs.	0.16	0.27-0.46	0.25
Length of post. segs.	0.25-0.40	0.40-0.75	?
Length of first seg.	0.46	0.46	0.80
Breadth anteriorly	0.48	0.46	0.80
Breadth posteriorly	1.11	1.11	1.30
Length of bothrium	0.07	Absent	?
Condition	Larval	Adult	Larval

Since the essential features of the internal anatomy of this species have been worked out by the European workers, only the striking similarities and differences to and from the data given in particular by Kiessling, Fuhrmann and Solowiow will here be dealt with in support of the writer's contention, in the absence of European material for comparison, that here in America we have the same species as that found in Europe. It will be considered that, as brought out by Lühe in three controversial papers (1897, 1897b, 1899a:715) and by Cohn (1898:126, footnote), *S. zschokkei* Fuhrmann 1898 is synonymous with *S. solidus*. As a matter of fact many of the data given below will be seen to compare more favorably with those published by Fuhrmann than with those by either Kiessling or Solowiow.

According to Kiessling the cuticula is from 15 to 18μ in thickness and divisible into two layers, of which the inner and lighter is from 8 to 9μ thick, while the outer is striated or granular. Fuhrmann described a cuticula only 7μ in thickness and divided into two layers, and Solowiow gave the thickness of the "homogeneous cuticula" as 23μ. Minckert (1905a:402) said that the comidian or pseudociliated layer, present in many bothriocephalids, was quite evident in *S. nodosus* but absent on the posterior borders of the proglottides. Here the cuticula was found to be 15μ in thickness, excepting on the posterior borders where it is only 5μ, and divisible into two layers, the outer of which, a little thinner than the inner, was much lighter, granular in consistency or somewhat striated with, however, a more or less uniform external boundary. It seems to be easily separated from the inner stratum, the bounding line, in reality the innermost portion of the external layer, being in most places very light. In fact the brightness of this inner layer of the outer stratum indicates the degree of separation of the two layers in the process of sloughing off the outer, which can be easily followed in sections as described by Kiessling. This description however, applies only to the adult stage. In larvae the cuticula, altho of the same thickness, shows an outer decidedly pseudociliated layer only 4μ in depth. The subcuticula, 88.5μ in thickness in the median line according to Solowiow, was found to be from 40 to about 65μ, Kiessling having given the limits as from 29 to 38μ. While the parenchyma is as described by the

authors, very fine meshed, calcareous bodies are present in comparatively small numbers, particularly just beneath the subcuticula of the larva. Their maximum dimensions are 23 by 13μ.

The musculature has been well described by Kiessling and Fuhrmann, so that it needs only to be added that in sections of mature proglottides the outermost layer of transverse muscles as well as the outer longitudinal layer are much less numerous and hence well defined than in the larva. Whereas Kiessling gave the thickness of the external and internal longitudinal groups, which on account of their compact nature were found to be more uniform in thickness than the transverse layers, as 8 to 33 and 16 to 49μ, respectively, and Fuhrmann as 4 and 8μ, the writer found them to be 17 and 30 to 40μ.

The nervous system was first studied in detail by Niemiec (1888:9) and later more thoroughly by Cohn (1898:126) who summarized its structure in the following words: "Von dem vordersten Theil, den Ganglien und der Commissur, ziehen die Hauptstränge und 12 Nebennerven rückwärts [six associated with each chief strand]. Die Nebennerven theilen sich dichotomisch in zwei Ebenen, der frontalen und radiären, ein Theil des Theilfasern rückt zwischen äussere Transversal- und Längsmuskeln, der andere bleibt weiter nach innen zu zurück, und diese Nerven treten einerseits unter einander durch Ringcommissuren, andrerseits durch radiäre Fasern mit den Hauptnerven in Verbindung." Kiessling gave the diameter of the chief nerve strands as 38μ and Solowiow as 67.9μ; here they were found to be from 30 in mature proglottides to 75μ in the anterior segments. The ganglia have a diameter of from 55 to 85μ, as compared with 77μ of Kiessling.

In transections from 25 to 30 excretory vessels appear in the medullary parenchyma with diameters ranging from 29 to 63μ. Fuhrmann gave 24 as the number, while Solowiow gave their size as 13.9 to 23.3μ. Foramina secundaria pierce the cuticula here and there, but they are not very numerous.

As indicated in the diagnosis of the subfamily the reproductive organs appear close behind the scolex. In one toto preparation of a larval specimen, number 72 of the above table, the earliest traces of their rudiments were present in the 18th proglottis, or 3.96mm. from the anterior end, while in the only mature specimen, H.7, they were in the 16th proglottis, a few eggs appearing in the uterus of the 17th. The cirrus and vagina open close together in a very shallow and sometimes quite obliterated genital cloaca having a maximum diameter of about 90μ, the vagina behind the cirrus, but only very slightly either to the right or left and not according as the uterine opening further back likewise alternates irregularly but with a greater amplitude. The three apertures form almost a right-angled triangle, as described by Kiessling; but, as was pointed out by Lühe (1899a:716) this arrangement is by no means constant but varies with the state of contraction or relaxation of the whole strobila and hence cannot be considered as specific.

The testes are arranged in a single layer in the dorsal portion of the medulla not only in the larva but also in the adult, as described by Fuhrmann, the majority of the excretory vessels being situated towards the ventral side of the

medulla. They are absolutely continuous from proglottis to proglottis. Their number in transections is from 30 to 40 (30 to 35, Kiessling) and in sagittal sections from 8 to 12 for each proglottis, thus making the total from 240 to 480 or over 300 on the average, which stands in distinct contrast with the number of about 100 given by Fuhrmann. The latter also gave their dimensions as 80 by 34μ, Kiessling as 16 to 66μ in young and 149μ in mature animals, and Solowiow as 68 to 93μ. The writer found them to be from 85 to 100μ in depth, 40 to 65μ in width and 55 to 85μ in diameter. They are, as indicated by their numbers, very closely crowded together in the proglottis. The vas deferens forms a compact mass of coils situated in the median line dorsally and slightly posterior to the vesicula seminalis to which it is closely applied as a sort of cap. While the diameter of the whole organ is about 0.3mm. that of the duct itself varies from 35 to 60μ when distended with spermatozoa. Kiessling gave its diameter as 38μ and Solowiow as 16.3μ. The large thick-walled seminal vesicle (Fig. 80) situated immediately above the cirrus-sac was found to have a maximum depth of 175μ and transverse diameter of 150μ, as compared with the 92μ of Kiessling and the 80μ of Fuhrmann. Its walls are very muscular, about 25μ in greatest thickness, and covered both internally and externally with numerous nuclei which are respectively epithelial and parenchymatous or myoblastic in their nature. Within the cirrus-sac the vas deferens is much coiled but not enlarged to form any secondary vesicle nor sharply separated into an ejaculatory duct and cirrus proper. The sac itself is oval in shape, the ventral end being the smaller, and the proximal end somewhat invaginated by the seminal vesicle. Its size is shown in the following table:

	KIESSLING	FUHRMANN	SOLOWIOW	THE WRITER
Depth	0.347mm.	0.25mm.	0.204mm.	0.185 to 0.203mm.
Width	0.192mm.	0.12mm.	0.174mm.	0.203 to 0.212mm.
Length	.....	.....	.....	0.166 to 0.185mm.

Its wall about equal in thickness to that of the seminal vesicle is, however, more open in texture, the myoblastic nuclei of the obliquely arranged muscle fibres being scattered thruout its diameter (Fig. 80). It is furthermore, not sharply separated either externally or internally from the surrounding parenchyma nor the numerous stout retractor muscles of the cirrus, respectively. The latter, in fact, constitute practically the whole of the contents of the sac apart from the duct itself. The only protruded cirrus seen had a length of 70μ, as compared with the 0.3945mm. given by Solowiow.

The vagina, the opening of which is usually situated about 50μ from that of the cirrus at the bottom of the shallow genital cloaca above mentioned, has a diameter of from 45 to 60μ at the first bend in its course within the medullary parenchyma. Soon after it enters the latter it becomes thin-walled, as pointed out by Fuhrmann, owing to the thinning out of the cuticula and the substitution of the proximal nucleated epithelium for the same, altho more peripherally much flattened nuclei are to be seen beneath the cuticula and crowded close to the basement membrane. In other words the gradual replacement from

within outwards of the cuticula for the original epithelium may be followed very easily in the walls of the vagina. The duct gradually enlarges to form a much elongated receptaculum seminis (Fig. 79) with a diameter of 92 to 104μ (9 to 21μ, according to Kiessling!) and sharply separated from the spermiduct, which, however, was not found to unite with the oviduct close to the dorsal transverse musculature as stated by Fuhrmann, but close to the ventral wall of the medulla. The ovary consists of two large wings (Fig. 79), composed of closely crowded tubules, lying immediately upon the ventral transverse muscles and united by a much smaller isthmus, the whole having a width of 0.64mm. as compared with the 0.28mm. of Solowiow. The average length and depth of the wings are, respectively, 105 and 90μ. Ova from the isthmus and more median portions of the wings of the ovary have a diameter of 13μ while their nuclei are 5μ. The respective measurements by Kiessling and Solowiow are 9 and 6μ and 13.9 to 23.3μ and 1.5 to 2μ. Fuhrmann stated that one of the most important differences between his *Sch. zschokkei* and *Sch. solidus* was the presence in the former of an oocapt, but Lühe (1899a:717) claimed that this structure was in all probability overlooked by Kiessling. It arises from the posterior aspect of the isthmus almost in the median line with a diameter of from 35 to 40μ. The oviduct, according to Kiessling has a diameter of 13, or to Solowiow of 27μ; here it was found to be from 25 to 30μ between the entrance of the vagina and that of the common vitelline duct, which two points are close together as in *L. intestinalis*. The common vitelline duct enlarges some little distance from its opening into the oviduct to form a vitelline reservoir having a diameter of 30μ (23μ, Kiessling). The vitelline follicles are extremely numerous and closely crowded together in a layer with a maximum thickness of 85μ, situated between the inner longitudinal and middle transverse muscles (Fig. 79). They are continuous at the margins of the proglottis as they are from joint to joint, and are broken only in limited elliptical areas above and below the reproductive ducts in the median line, as stated by Fuhrmann. The dimensions of the individual follicles are from 58 to 87 by 18 to 26μ, the larger dimensions being the dorsoventral diameters,—56 to 107 by 56μ, according to Kiessling, and 18 by 27μ after Solowiow. Just beyond the entrance of the common vitelline duct the oviduct enlarges to form the ootype with a diameter of 16μ (20μ, Kiessling) which is surrounded by the shell-gland, situated just above the median frontal plane and somewhat lateral. Thruout its course the oviduct is lined with an epithelium in which prominent nuclei but no distinct cell boundaries appear and from which numerous cilia protrude into the lumen. In the ootype these cilia are much more noticeable. From the ootype the oviduct passes ventrally with a few coils, then across the median line close above the receptaculum seminis as the beginning of the uterus. The latter gradually enlarges as it passes forward across the median line several times, until at about the middle of its course it has a diameter of 85 to 135μ. As regards the terminal portion of the tube it was found that, as Fuhrmann observed: "Der Endtheil der Uterus verengert sich und verläuft von der Dorsalfläche [the median frontal plane in which the last trans-

verse coil is situated] direkt ventral, um regelmässig abwechselnd links oder rechts neben der Vagina auszumünden."

Sections show that the actual opening is formed by the rupture of the bottom of a cup-like invagination of the cuticula from the ventral surface, which meets the end of the duct with a diameter of from 25 to 40μ. As Fuhrmann stated, "Dieser Ausführgang der Uterus ist von der Stelle an, wo er ins Rindenparenchym tritt, wie die Vagina und der Cirrusbeutel, von zahlreichen Parenchymmuskeln umhüllt und von einer der Körpercuticula ähnlichen Membran ausgekleidet;" but the cuticula seems to appear as such only near the opening, since only half-way back along this dorsoventral limb of the organ flattened nuclei are distinctly seen. In other words the flattened epithelium of the uterus, which, showing only a few scattered nuclei, was described by Kiessling as a "fine, structureless but elastic membrane," passes insensibly into the cuticula near the opening, no distinct line of junction between the two being discernible. This latter statement is likewise applicable to the similar structure of the vagina.

The dimensions of the ellipsoidal eggs in the sections of the uterus were found to be 62 to 65 by 33 to 36μ. Kiessling gave them as 49 by 37μ and Fuhrmann as 70 by 29μ. In discussing the latter, however, Lühe (1899a:718) remarked that not only did he find variations from 38 by 22 to 56 by 38μ in the size of the eggs in material of *B. zschokkei* sent to him by Fuhrmann, but that in general even greater variations than these are to be found in other species according to the various writers.

Our knowledge of the life-history of this species dates from the time of Abildgaard (1790) who, as mentioned above, was the first to experiment with the larval individuals found in fishes. Creplin (1829) united the two forms which were considered to be two separate species into one species, evidently on the basis of the previous work, especially Abildgaard's (cf. Donnadieu, 1877:340), while Donnadieu in his elaborate experiments on the life history of Ligula unfortunately did not differentiate between it and Schistocephalus. The development of the fertilized embryo into the oncosphere was first studied by Willemoes-Suhm (1869) and later more in detail by Schauinsland (1885:555), since when nothing of special importance has been added, so far as the writer is aware. Hence up to the present nothing is known about the development of the oncosphere into the larva in the intermediate host, as is indeed the case with most of the bothriocephalids.

As regards the identity of the material studied with the European species it will be seen from the above comparisons that, while there are many discrepancies among the data given by Kiessling, Fuhrmann and Solowiow, those by the latter departing the farthest in many respects, the resemblances so outweigh the differences as to make the erection of a new species unjustifiable. The thickness of the cuticula, the diameter of the excretory vessels, the dimensions of the seminal vesicle, the ovary and the eggs, which constitute the majority of the differences, might easily be explained by differences in age of the material studied. But the number of testes (100) as given by Fuhrmann

can scarcely be reconciled with that given here (300+), altho his dimensions of the organs agree with these perhaps better than do those by Kiessling or Solowiow. On the other hand there is another factor which may be in the long run more important than a comparison of the details of the anatomy of this evidently highly variable species, namely, the geographical distribution of the hosts. Altho little emphasis can be placed on Fabricius' finding *T. gasterostei* in the type larval host as long ago as 1780 in Greenland, it must be remembered that here in America there are, as in the case of *L. intestinalis*, a number of not only the same genera but also of the same species of the larval as well as of the adult hosts as in Europe. From this alone one would be justified in expecting to find the same species of Schistocephalus here, especially since it infests such a number of different host species. But it is a very surprising fact that apart from Linton's report of the larva from Montana evidently no one has up to the present found the form in any of the numerous fish-eating birds of the continent.

This evident infrequent occurrence of the species is illustrated by the fact that the material used for the present study consisted of only five lots: Nos. 61b and 72 from the body cavities of *Uranidea formosa*, taken from the stomach of *Lota maculosa*, and 190 from the coelom of *Gasterosteus bispinosus atkinsii*, of the writer's collection; one lot from *Gasterosteus cataphractus* from Alaska; and No. 17.192 of the collection of the University of Illinois from the intestine of *Lophodytes cucullatus*, the only mature specimen available.

HAPLOBOTHRIINAE Cooper 1917

Strobila formed by the subdivision of the segments of a primary strobila. Scolex of the latter a cylindrical, somewhat club-shaped organ bearing four eversible proboscides similar in structure to those of the Trypanorhyncha; scolex of the secondary (definitive) strobila merely the slightly modified foremost segment, provided with shallow dorsoventral depressions analogous to the bothria of other bothriocephalids. An elongated neck may be said to be present in the primary strobila. Segmentation of the primary strobila resulting in the formation some distance behind the scolex of a comparatively small number of long, narrow segments which in turn subdivide anteriorly to form the segments of the secondary strobila. Segmentation in the latter thus beginning immediately behind the secondary scolex, but complete in its anterior region only. Genital organs simple in each proglottis. Genital openings surficial, ventral and median as in the Diphyllobothriinae. Ovary and shell-gland median, respectively ventral and dorsal. Vitelline follicles in the medullary parenchyma, as are the testes, both within the nerve trunks. Testes separated into two lateral fields by the median excretory vessel and the genital organs in the median line. Vas deferens enlarged to form a large non-muscular seminal vesicle before entering the cirrus-sac. Cirrus armed with minute spines. Receptaculum seminis medium sized, sharply separated from the spermiduct. Uterus divided into a much coiled, proximal uterine duct and a large uterus-sac, as in the Ptychobothriidae.

Type genus: Haplobothrium Cooper.

Altho as yet comparatively little is known about the life-histories of the bothriocephalids, it has been shown that the definitive scolex and strobila develop directly from the larval stage, known as the plerocercoid, which is present in the intermediate host. This is certainly the case with Ligula, Schistocephalus, *Diphyllobothrium latum*, *Cyathocephalus truncatus* and Triaenophorus. As a matter of fact in all of these the scolex is more or less well formed before the larva reaches the final host; and after that the plerocercoid continues to grow and soon shows the beginnings of segmentation which mark the young strobila. Consequently the writer feels that what in the present paper is called the primary strobila of Haplobothrium must be looked upon as the true strobila, homologous to the young strobila of other bothriocephalids. This is contended in spite of the fact that what was formerly considered (Cooper, 1914, 1914a) to be the strobila is quite similar, apart from the absence of external segmentation in its posterior region, to that of other members of the order. Even tho it is provided with a very aberrant scolex region—and the scolex is no more sharply set off from the rest of the larva in other species, such as *D. latum*—the young unsegmented primary strobila may be considered to be a typical plerocercoid.

The nervous system is typical in that it consists of two chief strands united anteriorly by a commissure. The relatively large size of the latter, however,

seems to be due to the proximity of the highly specialized proboscides to which it sends large branches. The excretory system is likewise built on the typical plan, the posterior connections with the exterior being, in fact, quite like those of *B. scorpii*. On the other hand, the terminations of the nervous and excretory systems in the secondary strobila, both anteriorly and posteriorly support the view that the latter is not homologous with the strobila of other bothriocephalids. What was formerly described as the ring commissure must now be considered as merely a secondary formation due to the fusion of the severed ends of the chief strands; which statement is also applicable to the terminal vesicle of the excretory system. And this, in spite of the fact that the secondary scolex is quite similar to the true scolex of other forms in that it is supplied with two sets of muscles which are not found in the foremost segments, but are peculiar to the scolex.

Since there is considerable evidence in the literature on cestodes to show that the prominent posterior borders of the foremost segments of many species are developed as accessory organs of attachment or for locomotion (cf. Spengel, 1905:281), the question might well be raised whether external segmentation in Haplobothrium is palingenetic or cenogenetic in its nature, particularly since it is confined to the anterior region of the secondary strobila. The facts that no such appendages are present in the primary strobila and that the posterior end of the secondary one is not segmented, apart from the consecutive sets of genitalia, would seem to point to the original condition being one in which external segmentation was absent as in Ligula or Triaenophorus. Since, however, in the middle region of the secondary strobila there is an actual correspondence between the external and the internal segments, it is quite probable that the external segmentation is much older than might at first appear, while the ligulate condition of the posterior end may have developed secondarily. It is well to remember, too, in this connection that according to Lühe (1898:285) Ligula has descended from fully segmented bothriocephalids.

The subfamily, which up to the present contains only one genus and one species, bears a general resemblance to the Diphyllobothriinae. It differs from the latter, however, in that the genital organs are simple in each proglottis; the vitelline follicles are medullary; the testes are within (i.e., medial to) the nerve trunks; the seminal vesicle is not strongly muscular; the cirrus is armed with minute spines; the receptaculum seminis is medium sized; while the uterus is divided into a uterine duct and uterus-sac as in the Ptychobothriidae.

HAPLOBOTHRIUM Cooper 1914, e. p.

Haplobothrium Cooper 1914:1-2, 1914a:115

Borders of the terminal disc of the secondary scolex and of the posterior auricular appendages of both scolex and anterior segments provided with minute spines which disappear with the appendages farther back. Nervous system consists of two chief strands situated in the medullary parenchyma outside of the vitelline follicles, uniting in the anterior end of the secondary strobila to form a secondary nerve ring, and eight collateral strands, four arranged around

each main tract, the latter in the jointed portion of the strobila only, but in the true scolex to form an irregular transverse commissure situated among the proboscides. Excretory system composed of one large median and slightly dorsal vessel and two smaller lateral and ventral, all uniting in the secondary scolex behind the nerve ring to form a vesicle. No genital cloaca; opening of vagina close behind that of cirrus, towards the anterior end of the proglottis, that of the uterus much farther back. Sphincter vaginae present. Vitelline glands in numerous follicles arranged cylindrically around the testes, both continuous from proglottis to proglottis, leaving clear areas opposite the central genital ducts; large vitelline reservoir. Vas deferens provided with a sperm-reservoir at its posterior end near the middle of the proglottis; whole of the course of the duct dorsal to the uterus-sac. Uterus-sac when gravid occupies the whole of the middle of the proglottis.

Type and only species: *H. globuliforme* Cooper.

The genus is here emended owing to the elevarion to subfamily rank of a number of the characters given in my original generic description.

HAPLOBOTHRIUM GLOBULIFORME Cooper 1914

[Figures 9, 10, 43, 44, 65-67]

1914 *Haplobothrium globuliforme* Cooper 1914:2, 1914a:115

Specific diagnosis: With the characters of the genus. Small worms, primary strobila up to 70mm. in length, secondary to 110mm., with respective maximum breadths of 0.3 and 0.6mm. Primary scolex 0.35mm. in diameter, indefinite in length, bulbs 0.40 to 0.45 by 0.06 to 0.07mm.; secondary scolex, 0.4 to 0.5 by 0.25 to 0.4mm. Auricular appendages disappear at about the 25th segment in normal secondary strobilas. Foremost secondary segments tetragonal, middle and posterior much elongated and considerably depressed.

Cuticula 3 to 4μ in thickness, subcuticula 25μ. Chief nerve strands 18μ in diameter, narrowing intersegmentally. Terminal excretory vesicle 20 to 40μ in diameter.

Genital organs begin at about the 15th proglottis. Opening of cirrus and vagina 0.02 to 0.07mm. apart.

Testes spherical to ellipsoidal in shape, 70 to 115μ in maximum length; about 80 in each segment. Vas deferens median, elongated, only slightly coiled, 10 to 55μ in diameter. Vesicula seminalis broadly spindle-shaped, 140 by 90μ. Cirrus 20 to 30μ in diameter; cirrus-sac, 0.16 to 0.21 by 0.14 to 0.16 by 0.18 to 0.20mm.

Vagina 20 to 30μ in diameter at its opening, 56μ in its enlarged distal portion. Receptaculum seminis 30 to 45μ in diameter, spermiduct 5 to 10μ and very muscular. Ovary hippocrepiform, the limbs directed posteriorly and often fused with each other, the isthmus narrow. Ova from latter 10 to 12μ in diameter, their nuclei, 7μ. Oocapt 15 to 25μ in diameter, oviduct 8 to 15μ.

Two vitelline ducts, each 6μ in diameter; vitelline reservoir 25 to 55μ; follicles spherical or ellipsoidal in shape, 8 to 50μ in diameter, very numerous and closely crowded. Ootype 20μ in diameter; shell-gland irregular in shape, poorly developed. Uterine duct enlarged proximally with few coils, smaller distally and more coiled, median, 25 to 55μ in diameter; uterus-sac elongated, filling most of the medulla when gravid; uterus opening a small median elongated slit, situated near the posterior end of the sac.

Eggs, 60 to 70 by 40 to 43μ.

Habitat: In the intestine of *Amia calva* L.

HOST	LOCALITY	COLLECTOR	AUTHORITY
Amia calva L. (type host)	Go-Home Bay, Muskoka, Ontario	A. R. Cooper	Cooper 1914a : 81
" "	Havana, Illinois	H. B. Ward	Cooper (the present paper)
" "	Fairport, Iowa	"	"

Type specimen: No 33.1 in the writer's collection.

Co-types: Nos. 33.2 and 33.3 of the same, in the collection of the University of Illinois

In a preliminary paper on the systematic position of this species the writer (1914:1) described the scolex as ". . . unarmed, although the edges of the terminal disc and auricular appendages of both scolex and anterior proglottides are provided with very minute spines. Bothria, two shallow depressions on the dorsal and ventral surfaces, very simple in structure," and in the detailed description which followed (1914a) the organ was dealt with as follows (p. 82): "The scolex is quite small, simple externally, and with the unaided eye can scarcely be distinguished from the first joints. It is shaped roughly like a rectangular solid, hollowed out laterally to form simple depressions and dorso-ventrally the shallow bothria or organs of attachment. The summit is somewhat prolonged as a low pyramidally-shaped disc, quite comparable to that ("Scheitelplatte") found in the members of the subfamily Triaenophorinae Lühe 1899. . . . The opposite end of the scolex is modified to form two pairs of auricular appendages closely resembling internally as well as externally those of the foremost joints." Furthermore, in both papers it was emphasized that the scolex differs little in structure, apart from the nervous and excretory systems, from the first segments, and that the simple bothria seem of little functional importance as compared to those of other species while the auricular appendages of both scolex and foremost joints with their borders of minute cuticular spines probably act as accessory organs of attachment. Since then the latter view has been rendered still more highly probable, altho as yet no observations have been made on the living worms in their relation to the wall of the host's intestine, by the discovery that the so-called scolex (Figs. 9 and 10) is not in reality the scolex but only a slightly modified anterior segment.

The true scolex is something quite different from anything present in the whole order so far as the writer is aware. As shown in figures 43, and 44, it con-

sists of the slightly enlarged anterior end of the original plerocercoid or larva from which protrude four proboscides, the whole somewhat resembling a hydra and at once reminding one of the Trypanorhyncha. As will be presently seen the latter comparison is a very apt one. Each proboscis consists of a permanently protruded base or stump, as indicated in figure 43, about 85μ in length and 45 to 55μ in diameter, and an eversible proboscis proper having about the same diameter. The former is somewhat conical in shape and thickly set with minute, posteriorly directed cuticular spines which pass on to the neighboring portions of the scolex for a short distance. The whole forms at first sight a continuous tentacle gradually diminishing in size to the pointed end. These tentacles attain a length of 0.35mm., including the base, when fully evaginated, and are directed almost at right angles to the longitudinal axis of the larva, their bases being, however, turned slightly forward (Fig. 43). Within the scolex the tentacles are accommodated in elongated cylindrical muscular sacs which are quite comparable in structure to the bulbs of the Trypanorhyncha. These (the sacs) lie freely in the loose parenchymatous tissue in the diagonal diameters of the region. When the proboscides are invaginated, they have a length of 0.45mm. with a diameter of 0.07, or 0.40 by 0.06 when the tentacles are protruded. The walls of the bulb (Fig. 67) are composed of two thick layers of muscles, an outer longitudinal or somewhat oblique—much the heavier of the two—and an inner circular, and a cuticula-like lining, on the inner border of which in transections numerous flattened nuclei appear. The walls are attached to the edge of the stump, and these layers have the same relative arrangement as that of the cuticula and cuticular muscles on the outside of the body, only being in the reverse order. Continuous also with the edge of the stumps are the walls of the proboscis proper, which consist of a thin external layer of cuticula and only feeble cuticular muscles. Attached to the wall internally thruout its course are the retractor muscles of the proboscis which pass backward and become attached to the posterior end of the bulb. These can be seen best in longitudinal sections where the proboscis is retracted, for then they are closely crowded and much thicker, and their attachment to the inner end of the proboscis is nicely shown. In the retracted condition the latter is, of course, hollow, the narrow cavity often triradiate in transection (Fig. 67) being easily followed into the bulb for about one-third of its length. Closely applied to the cuticula of the tip of the proboscis appear in some cases gland-like cells taking the counterstain quite like those behind the bulbs to be described below. They are shown in figure 67. Apart from the structures already described, the contents of the bulbs and consequently of the proboscides to a certain extent, consist of a small amount of loose parenchymatous tissue and what is evidently a good deal of nervous tissue coming into the posterior end of the organ.

Evagination of the proboscides is evidently brought about by the contraction of the muscles in the walls of the bulbs, but the body wall in the vicinity of the latter probably greatly assists since its musculature is well developed. Some distance behind the posterior ends of the bulbs the latter consists of a

ring-like layer of loosely arranged main longitudinal fibres occupying the middle one-third of the radius of the nearly circular cross-section; no transverse fibres; but comparatively strong cuticular muscles, of which the inner longitudinal layer is the more pronounced. Farther forward this main longitudinal group gradually gives off small fibres towards the cuticula as they themselves diminish in number and size, until at the level of the hinder ends of the bulbs only a few of the latter fibres are left just beneath the subcuticula. An outer series at the same time forms a compact layer situated close to the longitudinal cuticular fibres (and hence outside of the subcuticular nuclei) but separated from them by a thin stratum of circular fibres. And this continues to the tip of the scolex, most of the remaining inner longitudinal muscles being located at the ends of the transverse and dorsoventral diameters of the transection. In the region of the bulbs the body wall is thus quite muscular, and in all probability assists the bulbs in evaginating the proboscides by compressing the whole of the parenchyma surrounding them. Between the bulbs and right beneath the tip of the scolex a few transverse and sagittal fibres are to be found, while just beneath the bases of the stumps of the proboscides the outer longitudinal muscles unite with the longitudinal cuticular fibres to form ∩-shaped loops surrounding the diagonal quadrants of the scolex which accommodate the bulbs. These loops are evidently for the control of the direction of the proboscis stumps.

Owing to the fact that, as originally stated by the writer (1914a:96), "there is a more or less definite point in the strobila, at or about the 15th proglottis, ahead of which the genital organs do not seem to develop and behind which in older strobilas they appear very quickly," and the further fact that not only do the auricular appendages of the posterior ends of the proglottides disappear at about the same place constantly, namely, at about the 23rd or 24th segment, it might seem that the (secondary) strobila is composed of a more or less definite and predetermined number of segments. But this is not the case, as will be seen presently when the method of formation of new proglottides is described. As a matter of fact segmentation in this species is carried on after an entirely novel plan, involving the formation of not only new segments but whole chains of them or, indeed, whole strobilas from the original larval or primary strobila as it is here called.

The original larva which resembles the bothriocephalid plerocercoid, excepting for the peculiar scolex, gradually elongates with growth, until between a length of 4 or 5mm. the first traces of segmentation appear in the hinder ends of cleared specimens as feeble aggregations of nuclei forming faint dark lines at regular intervals. In one specimen 4.8mm. in length five intervals were made out, the second last of which was 0.37mm. in length by 0.20mm. in diameter, while the last one was slightly larger and rounded posteriorly. These primary segments elongate with the growth of the strobila, and the constrictions between them gradually deepen as their anterior and posterior ends enlarge slightly, the former relatively faster than the latter. When a total length of strobila of about 10mm. is reached, the hindermost segment,

itself now about 1.5mm. in length, begins to show faint transverse lines in its anterior end, decreasing in intensity from ahead backwards. These are the earliest traces of the divisions of the primary segments into the secondary segments which will become the definitive joints of the anterior ends of the adult strobilas. In other words the original primary larva, plerocercoid or strobila, divides up into secondary strobilas which eventually separate from each other and grow into the adult chains as described above for the species. But long before separation takes place the entire development of the anterior segments with their characteristic posterior auricular appendages and the formation in particular of the first segment can be followed in these primary strobilas (Fig. 44). Whereas originally (Cooper 1914a:82, Figs. 5 and 6, Pl. V) attention was drawn to young scolices with only 5 to 8 segments, it was found in connection with the present study that the latter number, about 8 in external view or 16 or 17 in cleared specimens, is in reality that developed by the secondary strobilas before detachment from the original chain. The smaller strobilas are now looked upon as having been prematurely and accidentally separated from the posterior end of the primary strobila. The attachment soon becomes very slight, owing to the rapid deepening of the constriction ahead of the first segment, so that some time before the auricular appendages of the latter are fully delimited posteriorly very little manipulation of even alcoholic specimens, let alone cleared ones, suffices to break up the chain. However, there was found intact in the material at hand one primary strobila 88mm. in length, showing twenty secondary strobilas, including the undifferentiated anterior segments from which they are developed. Furthermore, the last two of these, 10.4 and 11.5mm. in length, showed in their posterior unsegmented portions the earliest traces of the rudiments of the reproductive organs. As has been already intimated the anterior segments form within the secondary or definitive strobilas by a gradual demarcation from head backwards, first internally in the parenchyma—actually as transverse layers of nuclei (Fig. 44) which will eventually form the posterior auricular appendages —and then externally as shown in the figure.

A continued search for evidence in connection with the question of whether or not there is in the secondary strobila a definite number of segments (external and genital combined) brought out further interesting facts. The number was counted in several young strobilas, evidently not long separated from the primary strobila, with the following results in the case of four typical specimens: (1) Length, 19mm., number of segments, 45; (2) 27mm., 29 or 30; (3) 26.5mm., 30 (the posterior ones here ripe as in the next specimen); (4) 41mm., 32 segments. It would seem from these data that there is a more or less definite number of segments, which might be considered to be about 30. But in No. 3 segments 9, 10 and 11 were not only much elongated but further subdivided anteriorly; while in No. 4 similar conditions were present in segments 10, 11 and 12, excepting that in the case of the eleventh the aggregations of nuclei indicating the subdivisions were in the posterior end. Similar elongated segments in still other strobilas show this condition in their middle regions.

Thus there is a tertiary subdivision of the secondary segments, which must, however, be considered as by no means as regular as the secondary subdivision of the original primary segments. These facts explain the aberrant nature of the strobila in this region, noted formerly by the writer, and the presence in material of chains showing anteriorly very young segments similar to those formed in the oldest attached secondary strobilas but posteriorly much older segments with well-developed auricles and farther back the typical mature proglottides of the ordinary strobila. Consequently it is probable that there is not a definite number of segments formed, but that further, irregular and evidently indefinite subdivision, resulting in the formation of an inconstant number, takes place chiefly in the middle portion of the anterior segmented region of what now must obviously be called the secondary strobila.

In the light of this method of segmentation certain facts in connection with the nervous and excretory systems that were previously considered to be very unique, to say the least, will now be explicable. In primary strobilas, even those that are youngest, the excretory system consists, as in the adult, of a larger median vessel and two lateral vessels which run backward and unite in the posterior end to form a plexus from which very many small vessels pass to the exterior by prominent foramina secundaria piercing the cuticula, much as described by Fraipont (1881:11, Fig. 7, Pl. II) for *Bothriocephalus scorpii*. In the youngest larva I have been able to find only the median vessel, which becomes greatly reduced in diameter about twice the length of the bulbs from the anterior end is present in the scolex. It forms a simple plexus among the bulbs anteriorly. In primary strobilas, however, in which segmentation has gotten well under way, all three vessels are quite prominent. They pass close to each other as well as to the chief nerve strands, when they traverse the constrictions between the developing secondary strobilas, where the median vessel is somewhat enlarged. As they near the anterior end of the worm they give off numerous branches of their own calibre, and when they meet the large ganglionic mass described below, diverge as four vessels (two on each side) and continue lateral to the bulbs to the tip of the scolex. Here after forming an open plexus among the anterior ends of the former, they unite in a single median frontal loop. As the constrictions between the secondary strobilas deepen all three vessels likewise become gradually constricted until eventually they are cut off, and the adult conditions are subsequently developed by the simple process of the turning in of both severed ends. And since in these younger forms the median vessel is considerably enlarged at the region of constriction, it remains thus in the hinder end of the adult strobila as well as in the first segment—as described and figured elsewhere by the writer (1914a:93, Figs. 12, 37)—while in the latter it is joined by the lateral vessels to form the characteristic terminal vesicle.

The nervous system of the primary strobila consists of two chief strands passing thruout the segments, a quite irregular commissure connecting them anteriorly, and a very large ganglionic mass situated some distance posterior to the proboscis bulbs. The chief nerve strands, which are quite indistinct

at different levels but constantly located in the median frontal plane, diverge as they meet the ganglionic mass in passing forward, and consequently opposite the bulbs come to lie close to the subcuticula laterally (Fig. 65). About 0.2mm. from the tip of the scolex they are united by a very irregular but comparatively large transverse commissure, from which large trunks pass to the neighboring bulbs both forward and backward. This commissure has a length or longitudinal diameter of about 0.10mm., while its maximum depth between the lateral pairs of proboscides is about 40μ. It gives off large branches anteriad to the lateral walls of the bulbs and caudad to the central walls. In the latter case a large branch leaves the median portion of the commissure, which is incidentally freely pierced with excretory vessels on each surface, and shortly divides into two, each supplying the central walls of one of the frontal pairs of bulbs (Fig. 65). The anterior branches likewise arise in a common trunk on each side, which is in reality the continuation of the lateral ganglionic enlargements of the commissure, but they supply the outside walls of the lateral pairs of bulbs. Imbedded in the commissure are numerous nuclei which, on account of their larger size than the neighboring parenchymatous nuclei, are probably ganglionic or nervous in their nature. Just behind the posterior ends of the bulbs and extending from 0.8 to 0.9mm. farther backwards (Fig. 43) there is a large mass of large nucleated cells which in transverse sections (Fig. 66) is seen to occupy the whole of the medulla (and about the whole of the section) excepting for the excretory vessels. These cells are roughly spherical in shape and have a maximum diameter of 25μ, their nuclei being 5μ. On account of their finely granular consistency and their taking the counterstain quite like the anterior nervous commissure they were interpreted as being ganglionic cells. And this view was supported on closer study by the discovery that they are not only united laterally with the chief nerve strands (Fig. 66), which can scarcely be distinguished from them at various levels, but with each other thru a complicated plexus of fine longitudinal strands which pass forward towards the bulbs and form around their bases an almost solid mass of fibrils (Fig. 43). From this mass large strands from 10 to 15μ in diameter pass into the bases of the bulbs, one for each, and are distributed among the retractor muscles of the proboscis which they evidently supply. In the youngest primary strobilas but not in the older ones, this mass of fibrils at the bases of the bulbs evidently connects forward by a few strands with the commissure.

Just as the definitive form of the anterior and posterior ends of the excretory system is explained by the separation of the secondary strobilas and the subsequent growing over of the ends, so is that of the nervous system, particularly anteriorly. As was noted by the writer (1914a) in connection with the preparation of the original description of this species and shown in figure 11, the nerve-ring is drawn out anteriorly into a point which is directly opposite a small conical pit in the tip of the scolex. This fact, as well as the relatively small size of the nerve-ring, is explained by the contraction of the free end of the "scolex" after separation and the growing together of the ends of the nerve strands to form the ring. The close association of the nerve-ring

and the terminal excretory vesicle is also comprehensible in the light of this method of development, for, since the nerve strands are situated close outside the lateral excretory vessels at the constrictions, they simply turn in towards the median line and unite immediately ahead of the junction of the latter with the median vessel.

As will be gathered from the foregoing description there is a most remarkable resemblance between the scolex of *H. globuliforme* and that of the Trypanorhyncha not only in the structure of the proboscides but also in the presence of the large mass of ganglionic cells associated with them posteriorly. Each proboscis consists of three parts: (1) a hollow tentacle, capable of evagination, (2) a short permanently protruded stump, armed with thickly set minute, cuticular spines, and (3) a comparatively elongated bulb. Of these parts (1) and (3) may be compared respectively with the proboscis and the bulb of Tetrarhynchus or Rhynchobothrius. The proboscis, altho not provided with any kind of armature, is nevertheless supplied with a group of well developed retractor muscles which are evidently analogous at least to the single retractor muscle of the Trypanorhyncha. The bulb is not only provided with a musculature arranged so as to diminish on contraction the volume of the organ, but is also lined with an epithelium-like layer comparable to that of the members of the latter group. But since the bulb extends to the point of exit of the proboscis, there is no part corresponding strictly to the proboscis-sheath of Tetrarhynchus altho the stump would at first sight seem to be such. Furthermore, the cells forming the large mass behind the bulbs in Haplobothrium which are here interpreted as ganglionic cells, bear not a little resemblance to those described by Braun (1896:1294) after Pintner (1880), Lang (1881) and Niemiec (1888) as associated with the bulbs of *Tetrarhynchus longicollis* (v. Ben.) (=*Dibothriorhynchus ruficollis* Monticelli) and considered by some to be ganglionic cells and by others myoblasts. The distribution of the large nerve trunks arising from the nerve commissure is also somewhat suggestive of conditions in a few of the tetrarhynchids (cf. Braun 1896:1293).

While the writer is not prepared to go further into this comparison he would like to emphasize the significance of the layers composing the walls of the bulbs in *H. globuliforme* in connection with the possible origin of these most aberrant structures. In discussing the homologies of the proboscides of the Trypanorhyncha Benham (1901) said: "It appears more probable (Pintner) that each proboscis has been developed by the deepening and modification of an 'accessory sucker' of some Tetraphyllidean as its relation to the bothridia and its mode of development closely agrees with these structures. Functionally too it is a perfection of the armature plus the accessory sucker of three forms [Acanthocephala, Nemertini, and Taenioidea]; whilst there is no doubt that the 'phyllidea' of the orders are identical." The fact that here the walls of the bulb, since they are composed of an outer layer of longitudinal muscles, a middle layer of circular fibres and an inner cuticular layer are not only comparable but directly continuous with the cuticula and cuticular muscles of the body wall and in the reverse order would seem to lend support to

Pintner's view. Simple invagination of the external layers of the body wall in development would account for these structures, while the proboscis with its retractor muscles might well be formed by the modification of the external layers of an "accessory sucker."

CYATHOCEPHALINAE Lühe 1899, e.p.

Scolex unarmed, not longer than broad, with two surficial sucking grooves, more or less fused with one another, or a single terminal one having a sucker-like structure. External segmentation little expressed or absent. Genital organs in each segment simple. Genital openings surficial, median. Vagina and uterus open into a common vestibule—in young proglottides near one another—lying behind the male opening and similar to the genital atrium of other cestodes, which may be surrounded by a sphincter-like musculature. The genital openings of the different segments do not open on the same surface, but alternate irregularly from one surface to the other. Uterus a coiled canal without uterus-sac. Sexually mature in the intestines of fishes.

Type genus: Cyathocephalus Kessler.

The above is Lühe's (1910:22) diagnosis modified to read "may be surrounded, etc." instead of "is surrounded, etc." in connection with the genital sphincter, since there is no such structure in the species described below.

CYATHOCEPHALUS Kessler 1868

Taenia (part.)	Pallas	1781
Taenia (part.)	Batsch	1786
Echinorhynchus (part.)	Zeder	1803
Cephalocotyleum	Diesing	1850
Cyathocephalus	Kessler	1868
Cyathocephalus	Grimm	1871
Monobothrium	Grimm	1871
Acrobothrium	Olsson	1872
Cyathocephalus	Zschokke	1884
Cyathocephalus	Loennberg	1889
Cyathocephalus	Kraemer	1892
Cyathocephalus	Olsson	1893
Cyathocephalus	Lühe	1889
Cyathocephalus	Braun	1900
Cyathocephalus	Lühe	1900
Cyathocephalus	Lühe	1910

Scolex a single, undivided, terminal, sucking organ, which in its form and structure no longer shows an origin from two fused surficial bothria. External segmentation only slightly indicated. Sphincter surrounding the female genital cloaca apparently little developed. Occurrence: In Teleosts.

Type Species: *C. truncatus* (Pallas, 1781).

CYATHOCEPHALUS AMERICANUS Cooper 1917

[Figs. 11, 82, 93, 99, 104]

? 1893	*Cyathocephalus truncatus*	Linton	1898:428
1917	*Cyathocephalus americanus*	Cooper	1917 : 35

Specific diagnosis: With the characters of the genus. Small cestodes, up to a length of at least 11mm. with a maximum breadth of 1.2mm. Scolex

funnel-shaped, 0.3 to 0.6mm. long and 0.5 to 0.9 broad, with revolute edges. Neck 1.0 to 1.8mm. in length. Segments twice as broad as long, terminal one rounded.

Cuticula 5 to 6μ in thickness, with neither hooks nor spines; subcuticula 25 to 50μ.

Ten to twenty sets of genitalia, beginning 1.5 to 2.0mm. from the anterior end. Strong tendency for the reproductive apertures to lie all on one surface of the strobila. Vagina opens behind the uterus. Neither papillae nor sphincters around the genital openings.

Testes in two lateral fields in the medulla of the anterior portion of the proglottis, 60 to 70μ in diameter. Coiled vas deferens anterodorsal to cirrus-sac; no seminal vesicle before entering cirrus-sac nor connective tissue sack surrounding the whole duct. Protruded cirrus 0.2mm. in length by 0.12 in diameter at base. Cirrus-sac ovoid in shape 0.20 to 0.23mm. in length by 0.17 in diameter; no retractors connecting it with the dorsal body-wall; large mass of glandular pigmented cells surrounding it dorsally and laterally.

Vagina 12 to 15μ in diameter; no sheath near its opening; receptaculum seminis 50 to 75μ. Spermiduct very short and narrow, 25 and 8μ respectively. Ovary tubulolobular, fan-shaped; wings extending dorsally and laterally around the ventral genital ducts; isthmus prominent, 0.18 by 0.10mm.; ova in same 13 to 15μ in diameter. Oocapt 25μ in diameter. Vitelline follicles continuous from proglottis to proglottis, forming a layer 90μ thick in the cortical parenchyma, 20 to 35 in transections. Shell-gland dorsal. Uterine rosette not surrounded by a muscular sac, but the organ is enveloped proximally by numerous glandular cells.

Eggs, 40 by 30μ.

Habitat: In stomach, pyloric ceca and intestine of the host.

HOST	LOCALITY	COLLECTOR	AUTHORITY
(?)*Coregonus clupeiformis*	Outer Id., L. Superior	J. W. Milner	Linton 1898 : 429
" "	Off Giant's Tomb Id., Georgian Bay, L. Huron	Cooper	Cooper (the present paper)
" "	Charlevoix, Mich.	"	"

Type specimen: No. 165A, in the writer's collection.
Co-type: No. 165B, in the collection of the University of Illinois.
Type locality: Georgian Bay, Lake Huron, off Giant's Tomb Island.

Altho the species described here is closely related to *C. truncatus* of Europe, it presents so many differences from that species, even barring some probable errors by Kraemer (1892), that it is considered to be new. Probably the same form was reported by Linton (1898:428).

As shown in the appended table where the largest specimens at hand are dealt with, this species is considerably smaller than the European species which ranges from 6 to 40mm. in length by 1.5 to 4 in width. Linton gave these measurements as 7 and 1.2mm.

The general shape of the body, however, is the same, as are the proportions of the scolex and proglottides. The border of the infundibuliform scolex (Fig. 11) is thickened and almost constantly rolled backward slightly as in the figures given by Zschokke (1884a, Fig. 9) and Kraemer (1892, Fig. 5). The funnel is about 0.22mm. in depth, and is usually filled with a plug of mucous membrane from the host's alimentary tract. The posterior limits of the scolex are difficult to define since the organ gradually narrows down and then as gradually enlarges again to form the neck. The latter is considered to include that portion of the anterior end of the worm between the narrowest region behind the scolex and the first vitelline follicles which are situated some distance ahead of the first cirrus-sac. The maximum breadth of the strobila is at the posterior end of either the first third or one-half. The segments are as described by various writers for *C. truncatus* about twice as broad as long, the last one, however, being rounded posteriorly and provided with a notch in the middle which accommodates the exit of the excretory vesicle. They are, furthermore, closely united, as pointed out by Linton (1898:429) when he said "The bodies of these specimens appear to be unsegmented, or, at least, with only very faint indication of division into segments." As a matter of fact numerous transverse wrinkles present in most specimens make it almost impossible without the external evidences of the inner genitalia to distinguish the limits of the proglottides. And in this respect they agree with *C. truncatus*, since Zschokke (1884:38) said concerning the segments: "Ils sont solidement fixés les uns aux autres, leurs limites sont difficilement visibles." The following table gives the measurements of four of the largest specimens studied:

Length	10mm.	9mm.	11mm.	7.5mm.
Maximum breadth	1.01	0.92	1.11	1.05
Length of neck	1.48	1.00	1.48	1.8
Breadth scolex, tip	0.55	0.53	0.74	0.64
" " , base	0.37	0.42	0.55	0.30
Length of scolex	0.42	0.33	0.61	0.50
Number of sets of genitalia	13	12	13	10
First cirrus from ant. end	1.85	1.66	2.25	2.01
Remarks	Toto	Toto	Toto	Sectioned

The cuticula is 5μ in thickness over the scolex as well as on the segments, and is divided into two layers, the outer of which is about one-half as thick as the inner and more or less irregular in structure. However, no such chitinous hooks as described by Kraemer (1892:10) for the cuticula of the lateral borders were seen, but the whole tissue is freely pierced with numerous foramina secundaria of the excretory system, which in *C. truncatus* Kraemer considered

to be the points of entrance of nutriment. The thickness of the cuticula, according to the same author, is 19μ, an outer irregular layer being 5μ and showing a sort of ecdysis ("Hautungsprocess"). This, however, may be simply the separation of the outer layer of the cuticula from the inner which often appears in sections, since he said, "Diese Auffassung wird dadurch erhärtet, dass sich an einigen Stellen dieser Belag nicht findet, dafür eine junge homogene Cuticula,"—the latter being then the inner homogeneous layer. At any rate, it is quite evident that the cuticula of *C. truncatus* is a much thicker tissue than that of the form described here—and no one else than Kraemer seems to have described it.

The subcuticula is comparable to that of *C. truncatus* in that it varies in thickness from 25 to 40μ. It is composed of considerably elongated columnar cells whose nuclei, 5μ in diameter, are as thick as the cells themselves. Scattered spaces in the loose parenchyma, which evidently accommodated calcareous bodies before they were dissolved in the fixing fluid, were found to be ellipsoidal to almost spherical in shape and to vary from 13 to 25μ in length by 7 to 18 in width. Linton stated that the calcareous bodies of *C. truncatus* are 10 to 20μ long, Zschokke that they are 8 to 10μ and Kraemer that their size is 30 by 18μ.

In general the musculature is as described by Kraemer, but all the groups are comparatively weakly developed (Fig. 82). The longitudinal layer, for instance, is only 20μ in thickness in the median line posteriorly and about 60μ in the neck region (76μ in *C. truncatus*) where the dorsoventral and transverse fibres are also much stronger than elsewhere. In the anterior part of the neck, particularly immediately behind the scolex, the fibres of the two latter series are much stronger, altho less numerous than farther back. Just ahead of the posterior end of the funnel they become arranged in an arcuate manner longitudinally as well as transversely. Then from there on to the tip of the scolex they gradually become more numerous as they concentrate around the funnel of the organ, of which they obviously act as constrictors. Antagonizing these are numerous weaker radial fibres, arranged as in *C. catenatus* Riggenbach (=*Diplocotyle rudolphii* Mont.) where they were considered by Riggenbach (1898:639) to be derived from the longitudinal muscles with which they are continuous at the base of the scolex. Altho they mingle freely among the latter, they are still quite separate from them. Thus the writer is inclined to the same view regarding their homologies in *C. americanus*, since it seems clear that the dorsoventral and transverse fibres, which might otherwise be considered to give rise to them, become modified to form the circular muscles of the scolex. As a matter of fact only a very few of the longitudinal muscles of the neck pass for a short distance beyond the bottom of the funnel; most of them are inserted in the latter, thus functioning with the radial fibres in enlarging the organ of adhesion. According to Riggenbach these radial muscles are apparently absent from *C. truncatus*. They were not described by Kraemer; but the enlargement of the funnel was considered to be accomplished by the contraction of the dorsoventral fibres (cf. his Fig. 1). The outermost layer of

circular and longitudinal muscles in the scolex, which are merely extensions of the cuticular muscles of the neck region, are not nearly so strongly developed as in *C. truncatus*. There is, however, in the neck region, particularly in its anterior portion, a series of outer longitudinal muscles which, altho situated in transections among the outer clear ends of the subcuticular cells and very close to the longitudinal cuticular fibres, are nevertheless quite distinct from the latter. At the base of the scolex they pass inwardly between the cells of the subcuticula and continue farther towards the anterior border of the funnel than do the inner or main longitudinal fibres. Posteriorly they diminish considerably in number but may readily be seen in the mature proglottides.

The nervous system is arranged in general as in *C. truncatus*; but the longitudinal trunks are only 26μ thick by 13 wide (0.345mm. according to Kraemer). In the neck they are scarcely enlarged to form ganglia, such as shown in Kraemer's Fig. 5, but each is divided into two distinct dorsoventral halves which gradually diverge as they pass on into the scolex to form four large nerves. There is no single transverse commissure connecting the main trunks behind the funnel of the scolex but instead a number of fine cross-connections which are often difficult to make out satisfactorily.

As regards the excretory system there is an inconstant number of longitudinal vessels in transection, evidently more than the six of *C. truncatus*, which do not occupy definite positions but anastomose freely with each other especially in the lateral portions of the medulla. In the scolex these vessels are smaller and the anastomoses are much more numerous, while posteriorly at least two pass into a quite irregularly shaped terminal vesicle, which, however, in the light of Wolf's (1906) findings cannot be considered to be a true terminal excretory vesicle. As above stated, foramina secundaria are quite numerous in the cuticula.

The reproductive organs appear quite close behind the neck, the vitelline follicles being situated from 1.3 to 2.3mm. from the anterior border of the scolex, and the first cirrus-sacs from 1.6 to 2.2mm. From 10 to 20 sets of genitalia were observed for this species. These follow each other closely and are not separated by any septa or other boundaries, the vitelline follicles being, in fact, strictly continuous from proglottis to proglottis. The openings of the cirrus-sacs vary from 0.45 to 0.75mm. apart, but as pointed out by Kraemer, these measurements are of little diagnostic value on account of the different states of contraction. As in *C. truncatus* the reproductive openings are all on one surface of the proglottis but alternate as a unit irregularly from one surface to the other. There is, however, a strong tendency for them to lie all on the one face of the strobila. This alternation also involves the ovary, the isthmus of which is arbitrarily considered in the cestode to be ventral. It usually lies on the same surface as the reproductive openings, so that when the latter passes to the opposite surface it moves accordingly. This alternation of the openings has, of course, been known ever since Pallas described *Taenia truncata* in 1781, but, so far as the writer is aware, no one has dealt with the relations between the openings and the ovary noted here. Concerning this matter Kraemer

said only: "Das Verhalten, dass die Geschlechtsorgane alternirend dorsal und ventral nach aussen münden, erinnert in gewisser Beziehung, an die alternierende marginalen Geschlechtsöffnungen verschiedener Fisch- und Vogeltaenien und wurde bereits von den ersten Beobachter, Pallas und Batsch erkannt, d.h., sie hatten auf beiden Flächen die fortlaufende Reihe der 'Punkte' wahrgenommen, ohne sie indessen als Ausmündungen der Sexualorgane zu deuten. Die neueren Beobachter haben sämmtlich dieses oben beschriebene Verhalten übersehen, und geben die Geschlechtsöffnungen als ventral gelegen an." But whatever is the stimulus which, during the very early stages of development of the sets of genitalia from their rudiments, causes the reversal of the whole proglottis, it would seem to be such at times as to fail to bring about the turning over of all parts of the rudiment. As shown in figure 104, which is a diagram of a sagittal series of seven proglottides including the terminal one, the cirrus and female genital cloaca of number three from the top have gone to the opposite surface while the ovarian isthmus, represented by the solid black disc in each segment, has remained on the same surface as those in segments 1, 2 and 4 in the immediate neighborhood. Here the stimulus which brought about the unisurficiality of the latter may have influenced the ovarian portion of the common rudiment of number three and caused it to lag behind, while the more peripheral rudiments of the cirrus, vagina and distal portions of the uterus were freer to move. This arrangement of the parts in the aberrant segment in question naturally causes considerable departures in the courses of the reproductive ducts from the normal.

The genital openings vary from 75 to 115μ apart, but again as pointed out by Kraemer these data are of very little specific value. The vagina and uterus open into a common genital sinus or cloaca, but unlike conditions in the European species the vagina opens constantly behind the uterus and slightly to one side and not ahead of it. Furthermore, neither papillae nor sphincter muscles are present around either or both genital openings in this species. The female genital cloaca, usually situated at the bottom of a depression and often on a low papilla, ranges from 30 to 60μ in depth. In frontal sections it is seen to be in the form of a transverse slit about 60μ in length, into the ends of which the vagina and uterus empty; that is, the vagina opens diagonally behind the uterus and usually to the right of it. It is lined by a direct continuation of the cuticula from the surface of the segment. The general habit of the reproductive organs is shown in figure 93, which is from a frontal section of a mature proglottis.

The majority of the testes are situated in the medullary parenchyma in two fields lateral to the cirrus-sac, or more strictly speaking, in the lateral portions of the region between the cirrus-sac and the ovary of the proglottis ahead, since they usually extend forward to the latter and backward to the anterior ends of the wings of the ovary of the segment to which they belong. While their shape is usaully spherical or somewhat flattened anteroposteriorly according to the condition of contraction of the segment, their maximum diameter is about 70μ. The coils of the vas deferens, altogether about 0.30mm. in dia-

meter, are accommodated in the somewhat confined space dorsal and anterior to the cirrus-sac, extending to the ovary ahead (Fig. 93). Whereas Kraemer gave the diameter of the duct as 0.133mm. or about eight times as large as just before it enters the cirrus-sac, it is only 45μ at the most in this species. Furthermore, it is not enlarged to form a seminal vesicle close to the cirrus-sac, as shown in Kraemer's figures 6 and 13, but gradually diminishes in size until as it pierces the wall of the latter its diameter is only 10μ. Nor is the whole vas deferens enclosed in a connective tissue sac, such as described by Kraemer. Within the pouch it enlarges considerably to form a thin-walled inner seminal vesicle, situated for the most part near the proximal end of the former but often lying alongside the cirrus proper. This portion of the duct may attain a diameter of 30μ even when empty. Then follows the cirrus proper which is sharply separated from the seminal vesicle; as a matter of fact it actually protrudes backward into the latter with a diameter of 10μ and for a distance of from 15 to 25μ. The extruded cirrus has a maximum length of 200μ, diameter at the base of 120μ, and at the tip of about 40μ. The thick cuticula covering the organ is decidedly roughened or irregularly "cleft," especially towards the tip, but not provided with spines of any kind. Incidentally, the protrusion of the cirrus on account of its size, results in the eversion of almost the whole of the contents of the sac. The length of the cirrus within the sac is at least 185μ, —it is usually bent once in its proximal portion—while its diameter varies considerably. The layer of parenchymatous and myoblastic nuclei surrounding the cirrus within the sac is about 10μ in thickness as compared with 5μ in *C. truncatus*. In sections of the extended cirrus most of these nuclei appear in the tip of the organ surrounding a good deal of the cuticula which still remains invaginated; but they are in all probability myoblastic as are others farther back along the course of the retractor fibres. In frontal sections the cirrus-sac is circular in outline (Fig. 93), its maximum diameter being 175μ, while in transverse and longitudinal sections it is oval in shape and the diameter (length of the organ) ranges from 200 to 230μ. The smaller end is directed ventrally. Its wall is comparatively thin, ill defined, and composed of a somewhat loose network of muscular fibres running irregularly obliquely in all directions, so that sections cut in any plane show them almost circularly arranged. Owing to this fact and to the further fact that its innermost fibres are not easily differentiated from the retractors of the cirrus proper which bulk largely in the contents of the sac, the wall is fairly difficult to locate with emission of the cirrus. The sac is furthermore not provided with any retractors connecting it with the dorsal body-wall as described by Kraemer for *C. truncatus*. Forming a sort of gland closely applied to that part of the cirrus-sac within the medulla there is to be seen, even in toto preparations, a comparatively large mass of large darkly pigmented polygonal cells (Fig. 93). In frontal sections they lie on each side of the sac but do not extend much beyond its anterior and posterior edges, the whole structure being thus shaped somewhat like a saddle. Each cell is elongate in shape provided with a well-defined wall, prominent tho not especially large nucleus, and very granular and highly pigmented cytoplasm,

the color of the pigment being dark brown. Altho they are very closely arranged around the wall of the cirrus-pouch and most of them are quite pointed towards the same, their function is pretty much a matter of conjecture; unless perhaps they are the much modified myoblasts of the muscles of the walls of the pouch. This is suggested by the intimate relations of the inner attenuated ends of some of them with the latter. No such cells have been described for the European species, so far as the writer is aware. It would seem, however, that certain "radiär gestellten, kolbenförmigen Drüsen," merely mentioned and figured by Linstow (1904:308, Fig. 26) as surrounding the cirrus-sac of *Bothrimonus pachycephalus* Linstow, are similar to these peculiar cells. But in the latter species they are evidently much less extensive than in *C. americanus*. Similar glandular cells were also described by Schneider (1902: 76) for *Bothrimonus nylandicus* Schneider.

From its opening which has been dealt with above the vagina proceeds dorsally almost at right angles to the surface of the proglottis, and then within the medulla turns backward with a few coils to expand into a comparatively enormous receptaculum seminis which, on account of its size, can scarcely be distinguished from one of the coils of the uterus. At the turn in its course the duct has a diameter of about 15μ and is lined with a continuation of the cuticula of the female genital cloaca, 5μ in thickness, and surrounded by a layer of circular muscles. As it passes above the ovarian isthmus its cuticular lining gradually diminishes in thickness, so that the seminal receptacle is provided with a very thin layer only. While the latter may have a diameter of 75μ slightly behind the isthmus of the ovary, it narrows down very abruptly before joining the oviduct to a very small spermiduct, 8μ in diameter and about 25μ in length. In distinct contrast with *C. truncatus* there is no "connective tissue and muscular sac" surrounding the beginning of the vagina, as described by Kraemer, but only the usual mass of nuclei, most of which are subcuticular in their nature. The ovary (Figs. 82, 93) is a tubulolobular organ, the limbs of which radiate from a ventral isthmus laterally as far as the nerve strands, anteriorly as far as the cirrus-sac, and dorsally thruout the whole of the medulla, thus surrounding the central connections of the genital ducts and the coils of the uterus (Fig. 93). The wings, in whose irregularly shaped tubules young ova in various stages of development are to be seen, connect with the rounded isthmus by narrow portions quite as described and figured by Kraemer, altho he evidently erroneously called the isthmus the "ootyp." The latter in this species has a width of 0.18mm. by a length of 0.10 as compared with the similar measurements of 0.19 and 0.07mm. in the case of *C. truncatus*. Ova from the isthmus measured from 13 to 15μ in diameter, their nuclei 7 to 8μ and their nucleoli 4μ, those of the latter species being 9 to 12μ according to Grimm (1871) and 15μ according to Kraemer who gave the diameter of their nuclei as 9μ. The oviduct begins with a rather short oocapt (Fig. 99), 25μ in diameter, and proceeds for only a comparatively short distance, with a diameter of from 15 to 20μ, before being joined by the spermiduct. A little farther dorsally it is met by the vitelline duct which comes from the ventral portion of

the medulla just ahead of the isthmus where it is formed by the union of a right and left duct as in *C. truncatus*. Thruout its dorsoventral course the vitelline duct is expanded to form a vitelline reservoir which may reach a diameter of 40μ. Immediately outside of the longitudinal muscles the vitelline follicles form a compact layer from 70 to 90μ in thickness (152μ in *C. truncatus*), continuous from proglottis to proglottis and broken only immediately around the reproductive openings. They range in diameter from 30 to 85μ, while their number in transverse sections varies from 20 to 35, 45 being given by Kraemer. From its point of origin to a short distance beyond the entrance of the vitelline duct, the oviduct is lined with epithelial cells showing prominent nuclei but indistinct boundaries, the whole being thus of the nature of a syncitium. But soon this epithelium becomes modified in that, as the duct continues with a few coils to the opposite side of the proglottis, its cytoplasmic portion gets quite thin, while the nuclei remain more nearly the same size relatively speaking. Then as it further enlarges dorsally the oviduct is surrounded by an inconspicuous shell-gland. However, no shell-gland such as described by Kraemer was found in this species. Beyond the ootype the duct, in reality the beginning of the uterus, is enveloped for a considerable distance by numerous unicellular glands which at first sight appear to constitute a second and voluminous shell-gland. This mass of glandular tissue is so extensive in fact, that it occupies in frontal sections about one-half of the posterior half of the uterine rosette (Fig. 93). The individual cells, of which it is composed, are comparatively short, stout and well defined, their nuclei being large and the nucleoplasm clear like the cytoplasm. Most of the coils of this tubular uterus, which may attain a diameter of 0.10mm. or more when filled with eggs (0.038mm. in *C. truncatus*), are situated just behind the cirrus-sac. Before reaching the opening, the position of which has been stated above, the tube narrows down quickly. Thruout its course it is lined with a much attenuated epithelium, the nuclei of which, however, stand out prominently towards the lumen. In this species there is no muscular sac surrounding the uterus, as described and figured by Kraemer.

The largest eggs in the uterus not in a collapsed state were found to be ellipsoidal in shape and 40 by 30μ in size. Linton gave their size when preserved in acetic acid as 50 by 32μ; while the measurements for *C. truncatus* have been given as 95 by 76μ (Kraemer) and 44 to 51 by 33 to 36μ (Lühe, 1910). Since most of the eggs seen in the uteri of the sections made were quite young, many of them not having gone thru the first cleavage as yet, the writer is of the opinion that the size of the egg of this species is probably about the same as that given by Lühe for *C. truncatus* in Europe.

Altho evidently no one has as yet studied the early stages in the development of *C. truncatus*, Wolf (1906) discovered that the intermediate host is *Gammarus pulex* and that the transfer to the final hosts is a direct one. As regards the life history of *C. americanus* the writer can only say that he is of the opinion that *Pontoporeia hoyi* (Stimpson Mss.) may later be found to be the intermediate host at least in Georgian Bay, Lake Huron, where it constitutes practically the only food of *Coregonus clupeiformis*.

In the above description it has been shown that this species differs from the well-known *C. truncatus* of Europe in a great many points, but in none so radically as the following: The absence of chitinous hooks on the cuticula of the lateral borders; the presence of radial muscles in the walls of the scolex, and of a number of fine nerve commissures connecting the chief nerve strands anteriorly instead of a single one; the vagina opening behind the uterus opening; the absence of papillae and sphincter muscles surrounding the genital openings; no enlargement of the vas deferens to form a seminal vesicle just before entering the cirrus-pouch; no connective tissue sac surrounding the whole of the coiled vas deferens; the absence of dorsal retractor muscles of the cirrus-sac, and the presence of the peculiar glands closely surrounding the pouch; no "connective tissue and muscular sac" surrounding the beginning of the vagina; the very different central connections of the genital ducts as regards the ovarian isthmus ("ootyp" of Kraemer); and lastly, the absence of any such "shell-gland" as described by the same author. Consequently it has been considered to be specifically different from the European form and given a new name.

The material studied consisted of three lots, Nos. 43, 165 and 382A of the writer's colllection from the stomachs and intestines of several specimens of *Coregonus clupeiformis* (Mitchell) from Lakes Huron and Michigan as listed above.

BOTHRIMONUS Duvernoy 1842, char. emend.

Bothrimonus	Duvernoy	1842
Bothrimonus	Dujardin	1845
Bothrimonus	Diesing	1850
Cephalocotylea	Diesing	1850
Disymphytobothrium	Diesing	1854
Diplocotyle	Krabbe	1874
Diplocotyle	Monticelli	1890
Bothrimonus	Monticelli	1892
Diplocotyle	Braun	1900
Bothrimonus	Braun	1900
Diplocotyle	Lühe	1900
Bothrimonus	Lühe	1900
Bothrimonus	Schneider	1902
Diplocotyle	Linstow	1903
Bothrimonus	Linstow	1904

Scolex with two surficial and almost spherical bothria whose forwardly directed apertures may be separate or more or less completely fused to form a single terminal opening, according to the degree of contraction of the ridge separating the two internally, the latter representing the tip of the scolex in other bothriocephalids. External segmentation completely absent. Female genital cloaca with more or less well developed sphincter. Vitelline follicles in the cortical parenchyma in two lateral fields.

Occurence: In species of Acipenser and in teleosts.

Type species: *Bothrimonus sturionis* Duvernoy.

As pointed out by Schneider (1902a:72) the two genera Bothrimonus and Diplocotyle were separated by Lühe (1900:10) only on the basis of the differences in degree of fusion of the apertures of the bothria at the tip of the scolex. As a matter of fact the remainders of the generic diagnoses are identical. Schneider stated that the material of his *B. nylandicus* showed that these differences were simply due to differences in degree of contraction and relaxation of the scolex and in particular of its termination which is the ridge separating the two openings of the bothria either externally or internally. With considerable retraction of this ridge or septum the two openings fuse to form one, while with relaxation of the same and contraction of the bothrial walls the apertures are more or less separate, according to the species present. While in none of the few specimens of the species described below were the openings fused, various stages in the formation of a single terminal and almost circular opening from the two otherwise separate openings were observed in some material from *Microgadus tomcod* which was, however, too young to be determined with certainty specifically. Consequently, it seems just with the present state of our knowledge of these forms to unite the two genera, Bothrimonus and Diplocotyle, and to retain the older name of Duvernoy, as done by Schneider but not recognized by Linstow (1903; 1904:308).

BOTHRIMONUS INTERMEDIUS Cooper 1917

[Figs. 6-8, 45, 81, 94]

1917 *Bothrimonus intermedius* Cooper 1917 : 35

Specific diagnosis: With the characters of the genus. Small cestodes up to 45mm. in length and 1.6 in breadth. Scolex almost spherical, 0.60mm. long, 0.75 wide and 1.0 thick. Bothria hemispherical, their apertures ordinarily not fused to form a single terminal opening. Strobila uniform in width from a short distance behind the scolex to the posterior end; 0.6mm. in thickness; more convex ventrally than dorsally.

Cuticula 5μ in thickness. Nerve strands 15 to 20μ in diameter; each divides into two branches sagittally before entering the scolex; transverse commissure diffuse. Four main excretory trunks in ripe proglottides, six farther forward passing into the scolex; all in the medullary parenchyma.

Reproductive organs 1.5mm. from scolex; up to 66 in number. Weak sphincter around the common female cloaca. Vagina opens close behind the uterine pore which is not quite in the median line.

Testes in two lateral fields and two layers between the excretory trunks, continuous from proglottis to proglottis; spherical in shape, 80 to 100μ in diameter. Coils of vas deferens anterodorsal to cirrus-sac, the duct 30μ in diameter. Cirrus-sac oval, 75 by 45μ; everted cirrus, 60 by 85μ.

Vagina 10μ in diameter; receptaculum seminis, 40 to 60μ; spermiduct, 10μ. Ovary crescentic in shape, wings tubulolobular; isthmus almost spherical, 0.1mm. in diameter. Oocapt 25μ in diameter, oviduct 15 to 20μ. Common vitelline duct 120 by 30μ. Vitelline follicles spherical, 60μ in diameter; in the lateral thirds of the strobila, continuous at the margins of the same and from

proglottis to proglottis. Shell-gland obscure. Uterus surrounded by glandular cells proximally; 0.25mm. in maximum diameter.

Eggs, 36 by 24μ in dimensions.

Habitat: In the intestine of *Pseudopleuronectes americanus* (Walbaum), the winter flounder, from Brandy Cove, St. Croix River, at St. Andrews, New Brunswick.

Type specimen: No. 206.1 in the writer's collection.

Co-type: No. 206.2 from the same, deposited in the collection of the University of Illinois.

Since 1842, when Duvernoy described *Bothrimonus sturionis*, the type species and the only one reported for America up to date from a specimen of *Acipenser oxyrhynchus* Mitchill (=*A. sturio* L.) collected by M. Lesueur in 1835, the following species have been found in Europe: *Diplocotyle olrikii* Krabbe (1874), *D. rudolphii* Monticelli (1890:205), *B. fallax* Lühe (1900b:257), *B. nylandicus* Schneider (1902a:72), *D. cohaerens* Linstow (1903:291) and *B. pachycephalus* Linstow (1904:307). As pointed out by Schneider (1902:77), *D. serrata* Linstow (1901:288) evidently does not belong to the genus at all. But with none of these could the material studied in connection with the present description be alligned. Altho it bears resemblances in individual points to *B. cohaerens* and to *B. pachycephalus*, doubtless owing to the fact that these have been better described than the others, including *B. fallax*, and closely approaches *B. nylandicus*, yet it is so different from the latter that it is considered to constitute a new species.

The scolex (Figs. 6-8,) is typical in that it is composed of two surficial and almost hemispherical bothria arranged in the usual manner. These are well separated not only posteriorly from the strobila but laterally from each other by distinct grooves as in *B. nylandicus*. In all of the specimens studied the apertures of the bothria, usually circular in shape and about 0.1mm. in diameter altho in a few cases somewhat elongated dorsoventrally, were distinctly separate. But since, as shown by Schneider, there is great variation in the extent of fusion of the two apertures owing to differences in degree of contraction even in individual species, this separation is not considered to be of specific, let alone generic, value. The compressed lumen of the bothrium has a transverse diameter of 0.3mm.; while the other measurements of the scolex are as given in the table below. The short unsegmented region between the scolex and the first set of genitalia, which has a length of about 1.5mm., may be considered to be a neck. Excepting for the openings of the reproductive organs and the protruded cirri, there are no external indications of segmentation. Internally this is also the case as regards the vitellaria and testes, which are both strictly continuous from proglottis (set of genital organs) to proglottis, as in the genus Bothriocephalus (*vide infra*). The strobila, which is quite uniform in diameter from the region close behind the scolex, is about one-half as thick as broad and slightly more convex ventrally than dorsally, as in *B. nylandicus*. None of the specimens at hand were complete posteriorly. The

following table gives measurements of the three largest specimens of the material studied:

Length	45mm.	38mm.	21mm.
Length of scolex	0.55	0.59	0.37
Length of bothria	0.64	0.72	0.66
Breadth of scolex	0.74	0.76	0.72
Depth of scolex	0.90	0.94	1.02
Width of strobila just behind scolex	0.87	0.87	0.74
Maximum breadth	1.34	1.34	1.60
Average breadth	1.16	1.16	1.2
Depth at middle	0.55	0.50	0.61

The cuticula is about 5μ in thickness not only over the general surface of the strobila but also in the interior of the bothria. In the latter situation it is divided into two layers comparable to those described by Schneider (1902a: 75) for *B. nylandicus*: an outer, occupying about three-fifths of the whole thickness and made up of comparatively long comidia or pseudocilia, and an inner, quite darkly staining stratum. Whereas Schneider stated that "Diese Härchen finden sich überall auf der ganzen Oberfläche des Cestoden mit alleiniger Ausnahme der beiden Hohlräume in den Saugnäpfen und der Rinne, welche den Scolex vom Rumpfe scheidet," the writer found that these were the very places the two chief layers were best seen.

The musculature is quite similar to that of *B. nylandicus* as described by Schneider. All of the series are about equally, but none strongly, developed and each consists of isolated fibres. The arrangement of the fibres in the scolex is quite like that of *Clestobothrium crassiceps*, there being, however, no sphincters controlling the openings of the bothria.

The main longitudinal nerves are situated in the median frontal plane and about two-ninths of the transverse diameter of the strobila from the margins, posteriorly as well as in the neck region. In transverse sections each strand varies considerably in size and shape, but it is constantly considerably compressed and has a transverse diameter of from 15 to 20μ. Anteriorly the system differs greatly from that of *B. nylandicus*. In the latter, according to Schneider, the chief strands bend outwardly at enlargements in the region between the scolex and body; and from each of these nerves are given off to the neighboring bothria and one main branch towards the tip of the region to unite with its fellow of the opposite side, thus forming a commissure which is bowed forward. In this species each main trunk divides from 0.25 to 0.40mm. behind the posterior borders of the bothria into two branches of equal size which continue forward in a strictly sagittal plane as they gradually enlarge. At about the middle of the bothria each of these four trunks gives off large branches to the lateral walls of the former, and then, while approaching the median line and partly fusing with its fellow of the opposite surface, sends off several small branches to those on the other side. The commissure is, therefore, not single but composed of a number of transverse connectives of varying size. The

transverse ridge between the bothria, which represents the tip of the scolex, is also supplied with a number of small nerves from this irregular commissure.

In ripe proglottides there are four main longitudinal excretory vessels situated roughly in the median frontal plane, two at the extreme margins of the medulla and two just within the nerve strands. Farther forward these divide into three on each side. The middle one of each lateral trio then divides dorsoventrally into two, while the innermost pair gradually diminishes in size and are soon lost. This leaves three on each side, arranged as a triangle with the base towards the median line and the apex outward. They pass into the scolex and anastomose to form an irregular plexus. But this arrangement of the main vessels is attended with a good deal of irregularity; nor is it the same on both sides of the median line. For *B. nylandicus* Schneider described only two main longitudinal trunks "which divide anteriorly into several canals and form numerous coils, especially in the suckers." The excretory system of *B. fallax* according to Lühe (1900b:257) is like that described here in that there is a triangle of vessels on each side anastomosing with each other and with the nearest ones of the opposite side; but in adition it shows two other vessels which " . . . verlaufen im Gegensatz zu den dünnwandigen Gefässen des Plexus im Inneren der Markschicht, in der frontalen Medianebene, und zwar der eine nach innen, der andere nach aussen vom Längsnervenstamm. Letzterer erinnert seiner Lage nach an die Verhältnisse bei den Dibothriocephalinen, insofern als die Mehrzahl der Hodenbläschen nach aussen von ihm liegt." It will also be seen that the arrangement of the excretory vessels in this species is quite different from that described by Linstow (1904:308) for *B. pachycephalus* Linstow, in which species there are fourteen main vessels situated in the cortical parenchyma among the longitudinal muscles. None of the specimens were complete posteriorly so that the disposition of the system in the true posterior end was not determined.

The reproductive organs appear about 1.5mm. behind the scolex almost completely developed. Their openings are in the median line and, unlike *B. sturionis* Duvernoy, all on the ventral surface, that is, on the same surface towards which the ovarian isthmus is situated (cf. *B. fallax* Lühe, 1900:10 and *Cyathocephalus americanus*, p. 57). Furthermore, while the male and female openings are from 0.09 to 0.22mm. apart, the sets of genitalia up to 66 in numbe, are 0.55 to 0.65mm. apart in the longitudinal direction, which distances are, however, of no great specific value owing to the different degrees of contraction and relaxation of the strobila. The female genital cloaca is an irregularly circular opening into which the vagina opens constantly close behind the uterus, as in *B. nylandicus*, but in the median line, the uterine orifice being in this case the one which is not exactly in line with that of the vagina and the cirrus but alternates irregularly from side to side. There is a weakly developed sphincter surrounding the common female cloaca. It seems, however, to be at least partly confined to the vaginal opening rather than to that of the uterus.

As in *B. nylandicus*, *B. pachycephalus* and *B. cohaerens* the testes are situated in the medullary region and in two narrow lateral fields continuous

from proglottis to proglottis. As a matter of fact, they are confined to the areas between the two pairs of the four main longitudinal excretory trunks mentioned above. They are usually almost spherical in shape with maximum diameters of 80 to 100μ. Transverse and sagittal sections show that, owing to the large size of the median reproductive organs, especially the large uterus, and their consequent inability to expand laterally, they are arranged in two pseudostrata which occupy the whole of the dorsoventral diameter of the medulla of the regions in question. These two tiers are, however, not nearly as extensive as in *B. pachycephalus* Linstow (1904:308, Fig. 26). The vas deferens is in the form of a narrow mass of coils, situated immediately anterodorsal to the cirrus-sac or slightly to one side, depending on the amount of distension and consequent approximation of the uterus of the same proglottis to that of the proglottis ahead. It also extends to the dorsal wall of the medulla; and its diameter is about 30μ. Just within the cirrus-sac the vas deferens is surrounded for a short distance by radiating gland-like cells, reminding one of those outside of the pouch in *C. americanus*. But there are no such cells outside of the cirrus-sac as described for *B. nylandicus* by Schneider. Then it gradually diminishes from a diameter of 35μ in the ejaculatory region, which immediately follows, or perhaps includes the glandular region, to about 20μ at the middle of the sac. From this point it enlarges quickly and takes on the cuticula and a series of circular muscular fibres to form the cirrus proper which in the distal portion of the pouch may attain a diameter of 50μ. The extended cirrus has a maximum length of about 60μ and diameter of 85μ. The cirrus-sac is oval in shape, the smaller end being outward and the major axis at right angles to the surface. Its depth is 0.25mm. while its diameter is 0.17mm. As in *C. americanus* its muscular walls are only weakly developed and hence not very distinctly separated from the parenchymatous tissue within and without. Apart from the duct the contents of the pouch consists of numerous parenchymatous cells and retractor muscles, the whole forming a quite compact structure.

Just within the medulla the vagina turns backward and continues ventrally and posteriorly with a few coils toward the ovarian isthmus. Whereas its diameter is 30μ near its opening, half way along its course this is reduced to 10μ and enlarged again to 40 to 60μ to form the seminal receptacle. Close behind and somewhat dorsal to the isthmus it again becomes sharply restricted to 10μ to form the spermiduct. Its whole course is quite as described for *B. nylandicus*; but in the latter there is evidently no enlargement to form a seminal receptacle or it was overlooked by Schneider, as indicated in his statement: "Sie passiert gleichfalls auf dem kürzesten Wege die Subcuticularschicht und die Muskelschichten, biegt dann in stumpfem Winkel nach hinten um und zieht, immer enger werdend, gegen den Ovidukt hin. In der Nähe des Eileiters wird sie so eng und dünnwandig, dass die Einmündungsstelle nicht genau festgestellt werden konnte." The ovary is like that of *B. nylandicus* in that it is crescentic in shape, the tubulolobular wings extending to the dorsal musculature and surrounding the uterine coils. It is, furthermore, comparable

to *C. americanus* in that these wings also pass forward from the isthmus—but only halfway along the sides of the uterus—and that the median region of the latter is spherical and somewhat larger than the lateral portions. From the anterodorsal aspect of this enlargement, which has a diameter of about 0.1mm., the oviduct arises as described and figured for *B. nylandicus*. The diameter of the oocapt is about 25μ, while that of the oviduct beyond its point of union with the spermiduct is from 15 to 20μ. The common vitelline duct, formed by the union close within the ventral musculature of a right and left duct, has a diameter of 30μ when filled with the yolk cells. The whole of the common duct, 0.12mm. in length, acts as a vitelline reservoir, while the right and left ducts usually contain a good deal of yolk close to their junction. As in *B. nylandicus* the vitelline follicles are arranged in two lateral fields in the cortical parenchyma, which are not only so restricted as to leave wide median areas free of them dorsally and ventrally but are continuous at the margins of the strobila as well as from proglottis to proglottis. Like the testes they are spherical in shape, closely arranged, and have maximum diameters of 60μ. The shell-gland, located just beyond the point of union of the common vitelline duct with the oviduct, is so weakly developed that it is all but absent. The opening of the common vitelline duct into the oviduct was not found to be "from the right side" as in *B. nylandicus* but irregularly from either side. Nor was there seen any distinct enlargement of the oviduct in the region of the ootype.

The first portion of the uterus is very thin-walled, and, especially when free of eggs, quite distinct from the distal portion which attains a diameter of 0.25 mm. The whole duct is so voluminous when filled with eggs that it occupies almost the whole of the medullary region of the proglottis and hence more than one-third of the transverse diameter and closely approximates that of the proglottides ahead and behind, thus crowding the other organs almost to the point of obliteration—and this in spite of the fact that its coils, mostly arranged in the sagittal direction, are very close together. The distal end of the duct gradually narrows down in passing ventrally to a diameter of from 35 to 45μ as it pierces the ventral musculature to open ahead of the vagina as above mentioned. No special enlargement of the tube just before its opening, such as was described for *B. nylandicus* is present in this form; but a considerable length of the proximal portion of the duct is surrounded by glandular cells quite similar to those of *C. americanus* (cf. p. 61).

The maximum dimensions of the eggs are 36 by 24μ as compared to 40 by 25μ in *B. nylandicus*.

As the above description indicates, this form comes closest to *B. nylandicus* Schneider, but it differs from that species in the following important points: It is considerably larger; the cuticula lining the bothria is the same as that covering the general surface of the strobila; the number and arrangement of the excretory vessels are quite different; the structure of the nervous system especially anteriorly is radically different; there are more than twice as many sets of genitalia; there are no gland-like cells just outside of the cirrus-sac; the vagina is expanded proximally into an elongated seminal vesicle; the open-

ing of the common vitelline duct into the oviduct is not from the right side only but from either side; the opening of the uterus, and not that of the vagina, is not strictly median but alternating irregularly from side to side, while there is no enlargement of the uterus just before its opening; and finally, but of least importance, there is no fusion of the bothrial apertures. Consequently it seems fitting to consider this form a new species.

The material studied consisted of two somewhat fragmentary lots, Nos. 205 and 206 of the writer's collection, from *Pseudopleuronectes americanus* (Walbaum), the winter flounder.

MARSIPOMETRINAE Cooper 1917

Scolex with two typical and fairly deep bothria and a terminal disc. External segmentation very distinct and regular. Opening of cirrus and vagina marginal, irregularly alternating; uterus-opening surficial, ventral, at the same level with the genital cloaca or very slightly behind it. Only one set of genitalia in each proglottis. Testes in medulla between the nerve strands. Muscular vesicula seminalis outside of the cirrus-sac absent. Receptaculum seminis large, sharply separated from the spermiduct. Ovary not exactly in the median line but slightly approaching the margin bearing the genital cloaca, ventral, as is the shell-gland. Uterus in the form of a sac developed by the enlargement inwardly of that portion of the duct passing thru the cortical parenchyma. Eggs without opercula.

Type genus: Marsipometra Cooper.

As regards the general form of the scolex and the facts that the genital cloaca is marginal and that a vesicula seminalis is absent, Marsipometra comes closest to the Triaenophorinae; otherwise, however, it is related to other subfamilies. External segmentation is distinct and very regular, a neck being present as in Diphyllobothrium and Bothridium of the Diphyllobothriinae. The uterus-opening is at the same level with the genital cloaca, and not ahead of it as in the Triaenophorinae. Furthermore, as in most of the subfamilies there is only one set of genitalia in each proglottis. The testes are situated in the medulla between the nerve strands as in the Haplobothriinae. Unlike the structure in the Triaenophorinae, the receptaculum seminis is large and sharply separated from its continuation, the spermiduct, which also obtains for the Ligulinae, Haplobothriinae, Diphyllobothriinae and Cyathocephalus. The ovary is comparable to that of Triaenophorus, Anchistrocephalus and Anonchocephalus (cf. Lühe, 1902:325) in that it is not exactly in the median line but situated towards the margin bearing the genital cloaca. As in the Triaenophorinae, however, the uterus "nie die sogenannte Rosettenform bildend, vor seiner Mündung meist etwas erweitert, ohne dass indessen diese Erweiterung verhältnissmässig so beträchtlich ist, wie die sogenannte Uterushöhle der meisten Ptychobothriiden." This latter difference is further emphasized by the fact that at no stage in its development is the beginning of the uterus, which might be considered at first sight to be a true uterine duct, sharply separated from the enlarged portion as in the Ptychobothriidae. The outstanding feature that the eggs are nonoperculate has been noted under the remarks on the family.

MARSIPOMETRA Cooper 1917

Dibothrium	Linton	1897
Bothriotaenia	Ariola	1900

Scolex unarmed, sagittate. Neck present; strobila flat, ribbon-shaped: proglottides almost rectangular, posterior borders only slightly projecting.

Nerve strands far towards the margins, dorsal to the cirrus-sac and vagina. Testes in two lateral fields united ahead of and behind the uterus-sac and central genital ducts. Vas deferens much coiled proximally, only weakly so close to the cirrus-sac. Receptaculum seminis very long. Ovary reniform, wings tubulolobular, isthmus thick. Shell-gland not in the middle of the genital complex but towards the cloaca, ahead of the ovary. Vitelline follicles numerous, not in two lateral fields but continuous from side to side in the anterior and posterior regions of the proglottis, situated among the body muscles. Uterus-sac pouched, occupying the whole of the medulla dorsoventrally but not transversely. Uterus opening towards the margin bearing the genital cloaca.— *μαρσιπίον* a little pouch; *μήτρα* the uterus.

Type species: *M. hastata* Linton.

Attention is here called to the great similarity between Marsipometra and Haplobothrium in that each is found in an isolated genus of fishes, respectively Polyodon and Amia, which in turn are relegated to isolated families and orders. As suggested previously by the writer (1914) in dealing with Haplobothrium, the unique and generalized nature of these two genera is doubtless due to the great age of their respective hosts. On account of the fact that it has a typical bothriocephalid scolex, Marsipometra would seem to be the younger of the two, for evidently a longer period of time must have been required for the development of the peculiar trypanorhynchous scolex and method of segmentation of Haplobothrium, if indeed both are not due to extreme degeneration comparatively speaking.

MARSIPOMETRA HASTATA (Linton 1898)

[Figs. 4, 5, 46, 47, 68, 83, 100, 101]

1898	*Dibothrium hastatum*	Linton	1898:431
1900	*Bothriotaenia hastata*	Ariola	1900:440
1917	*Marsipometra hastata*	Cooper	1917:36

Specific diagnosis: With the characters of the genus. Medium sized cestodes up to a length of 110mm. with a maximum breadth of 3mm. at the middle. Scolex with deep bothria and prominent posterior borders, 1.5 to 2.8mm. in length, 0.5 to 1.8mm. in width anteriorly and 1.3 to 2.0 posteriorly. Subcylindrical neck, 0.8 to 1.5mm. wide. First segments very short and wide, middle much broader than long and rectangular in outline, posterior ones quadrate to slightly longer than broad. Whole strobila much depressed.

Cuticula 5μ in thickness, subcuticula 40 to 50μ. Calcareous bodies 18 by 13μ. Longitudinal musculature weakly developed, that of scolex strong. Nerve strands 15 to 25μ in diameter. Four main excretory vessels in the strobila.

Genital cloaca 40 to 60μ in depth, at the middle of the margin of the proglottis, irregularly alternating; hermaphroditic duct present, also sphincter cloacae. Vagina opens immediately ahead of the cirrus.

Testes ellipsoidal, 60 to 90μ in diameter, 80 to 120 in number, arranged in a single layer in the medulla and interrupted only centrally. Vas deferens a circular mass of coils, 0.25 to 0.30mm. in diameter dorsal to the uterus-sac, or to one side of it. Seminal vesicle within the cirrus-sac, 50 to 60μ in diameter; cirrus proper slender, 0.20mm. in length, 8 to 15μ in diameter. Cirrus-sac elongate, flask-shaped, 0.35mm. in length, 110μ in maximum diameter.

Vagina 15 to 20μ in diameter; passes to median line ventrally, then dorsal to the uterus. Receptaculum seminis median, 90μ in diameter. Ovary reniform, tubulolobular, 0.45mm. wide and 0.18 long; isthmus thick, ventral. Oocapt 40μ long and 18 in diameter. Two ventral vitelline ducts; common vitelline duct 20μ in diameter. Vitelline follicles irregular in shape and size, forming a continuous layer around the proglottis excepting for median circular areas dorsally and ventrally. Shell-gland small, compact, 115 by 55μ. Uterine duct with only a few dorsoventral coils near the median line. Uterus-sac circular in outline, 1.0mm. in diameter, divided by deep incisions into 5 to 8 pouches; openings opposite the genital cloaca or slightly behind its level in gravid proglottides almost in the medial line.

Eggs, 45 by 36μ.

Habitat: Intestine of host.

HOST	LOCALITY	COLLECTOR	AUTHORITY
Polyodon spathula (type host)	Ohio R., Washington, Pa.	E. Linton	Linton 1898:431
" "	Ill. R., Beardstown, Ill.	H. J. Vancleave	Cooper (the present paper)
" "	L. des Allemands, Georgia	H. B. Ward	"
" "	Mississippi R., Keokuk, Iowa	H. B. Ward	"
" "	Mississippi R., Fairport, Iowa	H. B. Ward	"

Type specimen: No. 4724, Collection of the United States National Museum.
Type locality: Ohio River, Washington, Pennsylvania.

This species was originally described by Linton but with so little attention to the internal anatomy that up to the present it has remained pretty much a species inquirenda et incerta sedis, as pointed out by Lühe (1899c:40; 1900a: 106); altho Ariola (1900:440) placed it in the now obsolete genus Bothriotaenia Railliet.

Linton described the color of the living forms as " . . . at first lemon-yellow; after lying in water for a few minutes the bodies become colorless or faintly bluish translucent, while the heads remained yellowish." Regarding their method of attachment he said: "Two pits were found excavated in the mucous and submucous layers of the pylorus near the spiral valve, in which the heads of a number of *Dibothria* were inserted. The length of the worm was re-

corded by the same writer as from 25 to 78mm., while the maximum breadth was 2.7mm. As shown in the table below, the largest examined by the writer was one 110mm. in length with a maximum breadth of 3mm., which, however, showed the characteristic opaque white uterus-sac filled with eggs in only the last eight proglottides. The scolex (Figs. 4, 5) and strobila are, as described by Linton, ". . . sagittate (when at rest and contracted), terminated anteriorly with a button shaped tip [the terminal disc] which is bluntly rounded in front and marked off from the remainder of the head by a slight constriction, in life angled posteriorly; pits [bothria] variable in life but usually elliptical, often with anterior margin acuminate and sometimes with posterior margin indistinct. The head is angled posteriorly both laterally [surficially] and marginally, presenting a quite characteristic appearance in the living worm. Neck subcylindrical, narrower than the head. The segments begin some distance (6 or 8mm.) back of the head, as faint transverse lines. The first distinct segments are closely crowded much broader than long, median segments squarish [but still much broader than long], posterior segments usually a little longer than broad, rectangular, apparently separating rather easily. . . . Posterior angles of the segments slightly projecting. . . . Outline of most of the strobilas nearly linear and about the same breadth as the head. All the segments were remarkably regular in outline, no irregularities being observed." While this regularity in the form of the proglottides and in their gradual increase in size anteriorly and change of shape posteriorly is especially noteworthy in this species, the writer met with a few cases of intercalated triangular and aberrantly subdivided segments in the material studied. It should be emphasized, too, that the whole strobila including even the scolex is constantly much flattened dorsoventrally, which also assists in giving the worm the peculiar diagrammatic appearance which is mentioned below. The following table gives the measurements of four specimens, together with those by Linton in the first two colums for comparison:

Length	60mm.	45mm.	76mm.	39mm.	61mm.	110mm.
Length of scolex	2.75	1.85	1 48	1.75	2.34	2.01
Width term. disc	1.8		0.60	0.55	0.73	0.80
Depth term. disc			0.43	0 31	0.60	0.42
Width at base	2 0	1.7	1.35	1 31	1.83	1.95
Depth at base		1.3	1 16	0.96	0.98	1.10
Width of neck	1.1		0.87	0.88	1.40	1.52
Depth of neck		0 4	0.36	0.37	0.48	0.68
Length middle segs		0.35	0.75	0.46	0.80	0.73
Width of same	.	2.5	2.32	1.38	2.75	2.44
Length post. segs	1.13	0.55	1.5	0.85	0.90	1.52
Wikth of same	2.0	2.7	1.4	1.10	2.85	2.44
Maximum breadth			2.38	1.38	3.0	3.0
Measured in	water	alcohol	O.W.	O.W.	Alc.	Formol

The cuticula, 5μ in thickness, consists of two layers of equal thickness, an outer irregular and more darkly staining layer, which is sloughed off in many places, and an inner, more homogeneous and lighter stratum between which the outermost portion of the inner layer shows as a dark bounding membrane. Altho only about one-half as thick on the outside of the scolex and still thinner on the inside of the bothria, it is not modified to form minute spines on the edges of the terminal disc nor hinder end of the scolex where such might be expected to be located. Their absence also on the posterior borders of the proglottides (cf. *Haplobothrium globuliforme*) is not surprising since these protrude only very slightly. The subcuticula varies from 40 to 50μ in thickness and is made up of narrow elongated cylindrical cells with small nuclei, the outer ends of which are dendritic and quite separate from each other as are the bodies themselves. The meshes of the parenchyma are very loose and open, the spaces being large and the strands of the cytoplasmic framework considerably narrower than the small nuclei which are located as usual at the intersections but surrounded by only a limited amount of protoplasm. Linton stated that, "The segments contain numerous calcareous bodies, which exhibit a concentric structure." They are to be found fairly plentiful in all parts of the medulla and cortex and even among the subcuticular cells. They are elliptical or oval in outline, the largest having dimensions of 18 by 13μ.

The musculature of this species, excepting that of the scolex, is comparatively weak, no one series, not even the longitudinal, being especially strong. All groups are prominent, in that they consist of more or less isolated fibres quite diagrammatically arranged. Their conspicuousness is, indeed, amplified by the fine texture of the parenchyma. The frontal or transverse series do not form a compact layer closely applied to the inside of the longitudinal muscles but, as shown in figure 83, a stratum of varying thickness; owing to the degree of separation of the fibres, especially laterally. The myoblastic nuclei of many of them can be easily seen. The sagittal series are, however, quite prominent, and equally distributed from border to border of the strobila. They show their myoblastic nuclei and surrounding cytoplasm very clearly, reminding one of the dorsoventral muscles of *Abothrium rugosum*. While the fibres of both these series are only slightly more numerous opposite the posterior borders of the proglottides, where they form more or less distinct septa, they are very well developed in the neck and anterior segments. The longitudinal muscles form only a single layer of loosely arranged fascicles of irregular size in the middle and posterior segments, but in the neck they form a much thicker stratum, showing no distinct bundles and occupying the whole of the space between the transverse muscles and the subcuticular nuclei. Altho, as above mentioned, the posterior borders of the proglottides are not very prominent, there is a representative series of outer longitudinal muscles, best seen in the middle segments where they are situated close to the longitudinal cuticular fibres with which they are easily confused. Concerning the latter all that need be said is that they are well developed and consist of isolated fibres which render the two layers all the more visible.

The musculature of the scolex is, as might be judged from its size and its shape, very powerful. While the longitudinal muscles of the neck merely enter the base of the scolex, the transverse and sagittal fibres are directly continuous with the circular and radial fibres, respectively, of the latter. Here, however, the radial fibres are quite separate from the dorsoventral fibres with which they are considered to be homologous, especially laterally where they pass from the cuticula lining the bothria to the sides of the scolex as in other bothriocephalids with prominent bothrial walls. Farther forward the sagittal muscles proper passing between the bothria are scarce, their function being taken over by the very numerous and closely arranged radial fibres which are quite as plentiful in the median line as laterally. In the terminal disc both transverse and dorsoventral fibres are again prominent, while the radial ones are absent. Posteriorly the latter pass down along the sharp edges of the beginning of the neck. Frontal sections demonstrate the presence in the edge of the terminal disc as well as in the posterior borders of the scolex of two series of longitudinal arcuate fibres arranged for the control of these prominent ridges. These are perhaps modified portions of the outer longitudinal muscles which are very numerous in the scolex, and converge in the anterior portions of the edges of the walls of the bothria to become attached to the edge of the terminal disc at the four respective points.

The chief nerve strands, from 15 to 25μ in dorsoventral diameter and from 15 to 20μ in lateral diameter, are situated far towards the edges of the medulla and in the median frontal plane or somewhat dorsally (Fig. 83). They pass dorsal to the junction between the lateral and middle thirds of the cirrus-sac and consequently dorsal to the vagina. In the neck they are located in the very borders of the medullary parenchyma, but as they enter the base of the scolex they approach the median line somewhat. As they pass on with a varying diameter towards the tip of the scolex, they give off a number of branches to the walls of the bothria and finally enlarge in the terminal disc to form two ganglia, each with a diameter of about 50μ, which send off in turn numerous large branches to the immediate neighborhood. Each of these ganglia is divided into two large trunks which, however, continue only a very short distance farther forward before they are joined by two commissures to their fellows of the opposite side of the scolex in such a way that the two branches of the ganglia on each surface of the scolex are connected. In frontal sections each of these commissures is seen to be bowed slightly forward into the tip of the terminal disc and to give off further forward on each side a large branch which passes farther into the latter.

The excretory system consists of a varying number of vessels, of which four pursue a more or less constant course thruout the medulla of the strobila. These are found at all levels in transections and are separated from each other in the transverse direction by different distances. The outermost two, however, are slightly larger and have thinner walls than the innermost pair. They give off numerous large branches and are connected by various anastomoses with each other and the more peripheral vessels. In the neck they cannot be

followed as well, while close to the scolex they lose their identity and break up into a plexus of very small vessels which ramifies forward thruout the latter. In the posterior border of the scolex, however, a small branch on each side takes a straight course just within the nerve strand for a short distance. Flame-cells are quite numerous and readily discernible especially in the medullary parenchyma. In young strobilas where no segments have yet been lost, two comparatively large excretory vessels pass backward to the posterior end and empty into a small narrow terminal vesicle. This in a larva 12.4mm. in length was found to be 40μ long by 10μ wide, while the diameter of the excretory vessels was 15μ.

The earliest traces of the reproductive organs in the form of a transverse line in either half of the proglottis (the rudiments of the vagina, cirrus-sac and lateral portions of the vas deferens) appear from 4 to 10mm. from the tip of the scolex, while the first eggs are seen in the uterus-sacs from 25 to 35mm. from the same point. The development of all of the genitalia is very gradual and can be easily followed in good toto preparations, since the diagrammatic nature of the worm, above mentioned, extends to the reproductive system, making this species an ideal one for study. The cirrus and vagina open into a common genital cloaca, which is situated in the middle of the margin of the proglottis, while the uterus opens on the ventral surface, not in the median line but towards the side occupied by the atrium. The cloacae alternate irregularly from side to side, from one to ten having been found occupying the same margin in successive proglottides. The following figures represent the number of such segments before the genital aperture changes to the other side in the fifth specimen of the above table: 1, 2, 1, 8, 1, 1, 1, 2, 2, 3, 3, 1, 2, 2, 10, 1, 1, 1, 3, 3, 2, 2, 1, 4, 1, 1, 2, 2, 3, 2, 2, 3, 6, 6, 1, 1, 1, 1, 1, 3, 2, 1, 3, 3, 2—as far forward as the rudiments could be conveniently traced. The genital cloaca (Figs. 100, 101) is elliptical in outline when viewed from the side, its longer diameter being directed dorsoventrally, while in transverse sections it is squarish in outline. The dorsoventral diameter, longitudinal diameter and depth are, respectively, 70 to 85μ, 40 to 55μ and 40 to 60μ. Into the middle of the bottom of this depression opens the hermaphroditic duct which is about 60μ in length, into the bottom of which in turn opens the vagina immediately ahead of the cirrus. Since the cirrus proper is a long slender tube and since the external portion of the hermaphroditic duct is usually found quite tightly closed and the end of the cirrus turned around toward the opening of the vagina, self-impregnation would seem to be quite probable in this species. On the other hand, the fact that the genital cloaca is so well formed and further that it is surrounded by a well developed sphincter and a series of muscular fibres radiating out into the surrounding parenchyma, as shown in figures 100 and 101, argue in favor of its use in cross-fertilization. No protruded cirri were seen, however, in the material at hand. Perhaps both methods of fertilization occur.

The testes are spherical to ellipsoidal in shape, their longest diameters being dorsoventral, while their cross-sections are usually circular in outline. In segments where there are as yet only a few eggs in the uteri their dorsoven-

tral and transverse diameters are, respectively, 85 to 90μ and 60 to 80μ. In the anterior and posterior ends of the proglottis—they are not continuous from segment to segment but separated by the aggregations of sagittal and transverse muscles mentioned above as forming more or less complete septa—they form a single layer situated in the medulla in the median frontal plane, but are widely separated in the middle of the proglottis by the central genital organs and ducts, especially the uterus-sac. Their number ranges from 80 to 120 for each proglottis. While the wall of the testis consists of a very thin membrane from which nuclei protrude inwardly, the contents are such as to show the process of spermatogenesis quite clearly. The vas deferens forms a circular mass of coils, 0.25 to 0.30mm. in diameter, applied like a cap to the dorsal side of the developing uterus-sac and thus close to the inner end of the cirrus-sac. When the uterus becomes gorged with eggs it is pushed aside somewhat but still retains similar relations with one of the pouches of the former, located in the direction of the genital cloaca (Fig. 68). In the mass of coils the duct is usually distended with spermatozoa to a diameter of 40μ. It gradually narrows down to a diameter of 15μ before entering the cirrus-sac, before which there is, however, no seminal vesicle. But within the pouch the vas deferens enlarges to form a large seminal vesicle, which with a diameter of from 50 to 60μ takes only a few coils before passing on as the cirrus proper from which it is sharply separated (Fig. 101). The cirrus is a slender tube from 0.17 to 0.22mm. in length within the pouch and from 15μ in diameter nearest the seminal vesicle to 8μ at its opening. It is lined with a thin cuticula which is circularly cleft in its proximal one-third but almost smooth for the rest of its length, nowhere, however, showing anything in the nature of an armament. The cirrus-sac (Fig. 101) is an elongated flask-shaped structure with a maximum diameter proximally of 110μ and distally of 40μ, and a length of 0.35mm. The neck of the organ usually shows a couple of dorsoventral curves, while about 20μ of its distal end protrudes into the hermaphroditic duct. Its walls are comparatively thin and composed of an inner layer of circular muscles and an outer weaker and much less compact layer of longitudinal fibres. Apart from the seminal vesicle which occupies almost the whole of the proximal enlarged portion and the narrow cirrus, the contents consist of only a limited amount of parenchymatous tissue and a very few feeble retractor muscles. The whole structure of the cirrus-sac is in fact such as to suggest that the function is that of an organ for the explusion of spermatozoa rather than for the emission of a copulatory organ; altho a few muscles passing from the body wall around the cloaca to the anterior part of the neck of the sac (Figs. 100, 101) would seem to indicate that a small portion at least of the cirrus is protruded, perhaps during self-fertilization.

Altho the vagina opens into the hermaphroditic duct directly ahead of the cirrus, it almost immediately curves around the distal portion of the cirrus-sac to the anteroventral side of the latter which it follows closely towards the median line. Close to the wall of the inner end of the cirrus-sac, however, it crosses the distal coils of the vas deferens towards the dorsal sufrace and

skirts the uterus-sac. When it reaches the median line above the sack it turns sharply downward and backward. The vagina has a diameter of from 15 to 20μ opposite the middle of the cirrus-sac and is lined with only a comparatively thin layer of cuticula. It very gradually expands after crossing the inner end of the cirrus-sac to form a much elongated and very spacious receptaculum seminis, the diameter of which close to its inner end may be as much as 90μ. This is usually filled in sections with spermatozoa, a stream of which may often be seen passing on into the spermiduct. The beginning of the duct is surrounded by a poorly developed layer of circular muscles which are almost absent from the inner expanded portion. The receptaculum is sharply separated from the spermiduct which has a diameter of only 15 to 20μ and a length of 0.12mm. The latter is an almost straight tube passing in the median line from the more dorsally situated receptaculum to its point of union with the oviduct close to the ventral wall of the medulla (Fig. 83). It shows best in transections where its walls are seen to be composed of an epithelium of cubical cells lying on a distinct basement membrane, and to be surrounded with a thick layer of nuclei and extremely few, if any, muscle fibres. The ovary (Figs. 68, 83) is a somewhat kidney-shaped tubulolobular organ situated in the posterior half of the proglottis behind the developing uterus-sac with its concavity directed forward, and not exactly in the median line but slightly approaching the cloaca. It averages 0.45mm. in width by 0.18 in length. The isthmus, which is almost as long and about one-half as thick as the wings, is located only slightly below the median frontal plane of the medulla. Ova from the same have a diameter of from 20 to 25μ. In gravid proglottides where the uterus is filled with eggs only a small portion of the degenerating ovary remains, and this is accommodated between the two hindermost pouches of the uterus-sac. The oviduct commences in the median line anteroventral to the ovarian isthmus as a somewhat cylindrical oocapt, 40μ in length by 18 in diameter and not sharply separated from the rest of the duct (Fig. 83). It passes ventrally with a diameter of 20μ for about 50μ before being joined by the spermiduct, and then for only a short distance farther anterolaterally along the ventral transverse musculature before meeting the common vitelline duct. The latter is formed by the union in the usual manner of two vitelline ducts coming from the lateral regions of the proglottis along the ventral wall of the medulla. It is quite short, however, and usually contains only a limited amount of yolk, its diameter being at the most only 20μ. The vitelline follicles (Fig. 83) are irregularly ellipsoidal in shape, and situated either just within the transverse muscles, between them and the longitudinal muscles, among the latter or even slightly outside of the longitudinal muscles. While they vary considerably in size and, not being very numerous, are widely spaced, their average maximum diameter is about 50μ. They form a continuous band completely surrounding the medulla, excepting for irregularly circular areas above and below the ventral ducts and organs, in the median line, but are not continuous from joint to joint. On the whole they remind one of the vitellaria of *A. crassum*. The union of their different ductlets can be easily traced,

especially in frontal sections of younger proglottides, since they are comparatively large and hence quite distinct. The shell-gland is a small compact organ, about 115μ in width by 55μ in length, surrounding the oviduct just beyond the entrance of the vitelline duct, or to be more exact, just beyond the first turn taken by the latter in its return to the median line after passing laterally, as above stated. It is thus situated ventrally and a short distance from the median line. Beyond the shell-gland the oviduct continues as the uterine duct which takes only a few dorsoventral turns near the median line before emptying into the uterus-sac. The latter is formed in development by the gradual enlargement dorsally of that portion of the duct which traverses the cortical parenchyma on the ventral surface of the proglottis. Just before eggs appear in the sac this part of the tube can be seen in transections as a spindle-shaped dilatation, whose nucleated epithelial wall is surrounded by a thick layer of nuclei, the whole being, however, not distinctly separated from the proximal portion of the tube (the uterine duct of older stages) at a constriction just within the transverse musculature. In proglottides farther ahead this constriction is outside of the transverse muscles in the cortex; so that the uterus-sac must be looked upon, then, as being formed by a gradual enlargement of the distal end of the uterus as it becomes filled with eggs and not as a sac separated in the rudiments from the proximal uterine tract as in the Ptychobothriidae. In one case where only 5 or 6 eggs appeared in the lumen the uterus-sac had a diameter in frontal sections of 80μ; in the next segment following it was enlarged in all directions, somewhat elliptical in outline, with a diameter of 240μ; in the next still larger; and in the fourth somewhat pointed anteriorly. From this region on it quickly enlarges until finally it forms a capacious sac, as much as 1.0mm. in diameter, occupying in gravid proglottides the whole of the dorsoventral diameter of the medulla and almost all of the longitudinal and transverse diameters. In transverse sections it is almost entire in outline, while in frontal sections it is divided into from 5 to 8 large irregularly shaped lobes or diverticula, the hindermost two of which enclose the remainder of the ovary and the central connections of the reproductive ducts, as above mentioned. Ventrally, the sac is funnel-shaped towards the small opening which only appears when the proglottis becomes quite gravid. Since the uterus-sacs, even the most gravid ones, are not situated exactly in the median line but towards the margins bearing the genital cloacae, the openings form " . . . a zig-zag line of minute pores [which] traverses the median region of one of the broad faces of the strobila, each pore being near the middle of its segment." Linton correctly considered them to be for the escape of the eggs. Anteriorly, where the uterus-sacs do not yet contain eggs, these pores—in reality the ventral funnel-shaped portions of the sacs—are located about 0.18mm. on each side of the median line, but posteriorly they are relatively much closer together, in fact almost exactly in the median line. Furthermore, they are situated directly opposite or slightly behind the level of the genital cloaca. The opening is formed by the rupture of the body

wall in a very small and limited area, and not of a preformed membrane as in the Ptychobothriinae.

Concerning the eggs Linton (p. 433) said: "The ova are nearly spherical, with thin shells. They are about 0.04mm. in the greatest diameter." Those from material preserved in formalin were found by the writer to be sometimes spherical in shape but usually ovoid or ellipsoid, with maximum dimensions in the latter case of 45 by 36μ. Neither in sections nor in preparations of eggs from the uterus sacs of material in formol, alcohol or cleared in oil of wintergreen were opercula to be found, but at the one pole of the egg a small boss about 5μ in diameter which is often enlarged to form a distinct projection or appendage. Altho development had not progressed in any of the eggs studied so far that the six hooks of the oncosphere were visible, the writer is of the opinion that even in mature eggs no opercula would be found, since its almost spherical shape and the presence of the button-like thickening at one pole are quite like conditions in the nonoperculate egg of *Abothrium rugosum*, for instance, as described and figured by Schauinsland (1885:527) and further, since in the egg of the operculate type, as in that of *D. latum* or of *T. nodulosus*, described and figured by the same writer, the operculum is present long before the hexacanth embryo has developed.

As regards the life-history of this species nothing is as yet known. It is noteworthy, however, that very young larvae, such as shown in figures 46 and 47, can be easily recognized on account of the peculiar character of the scolex, so that it would not seem difficult to pick them out of the intermediate host whatever that may be. All sizes from the youngest (Fig. 46) to the largest were present in the material studied.

The material of this species consisted of Nos. 4724 and 4783 of the collection of the United States National Museum, Nos. 16.292, 16.421 and 17.11 of the collection of the University of Illinois and No. 154 of the writer's collection, all from the intestine of *Polyodon spathula*, the paddlefish.

TRIAENOPHORINAE Lühe 1899

Scolex armed or unarmed, always with two typical and not very deep bothria, ahead of which the flattened termination of the scolex projects more or less prominently in the form of a ring. External segmentation present or absent, in the former case an unjointed neck being absent. Opening of cirrus and vagina marginal, irregularly alternating; uterus opening surficial, ventral, ahead of the marginal genital aperture. Genital apparatus always single in each proglottis. No muscular bulb (Eschricht's body) on the inner end of the cirrus-sac. Receptaculum seminis comparatively small, not always sharply separated from the narrow inner end of the vagina. Uterus a much coiled canal, which while never forming a rosette is usually somewhat enlarged before its opening.

Sexually mature in the intestines of fishes and marine turtles; larval conditions mostly unknown.

Type genus: Triaenophorus Rudolphi.

TRIAENOPHORUS Rudolphi 1793

Vesicaria, Cysticercus et Taenia (omn. part.)	Auctorum	
Triaenophorus vel Tricuspidaria	Rudolphi	1793
Tricuspidaria	Rudolphi	1793
Triaenophorus	Rudolphi	1793
Rhytelminthus (part.)	Zeder	1800
Rhytis (part.)	Zeder	1803
Tricuspidaria	Rudolphi	1802
Tricuspidaria	Rudolphi	1809
Triaenophorus	Rudolphi	1809
Tricuspidaria	Rudolphi	1810
Tricuspidaria	Lamarck	1816
Triaenophorus	Rudolphi	1819
Triaenophorus	Creplin	1839
Triaenophorus	Dujardin	1845
Triaenophorus	Diesing	1850
Triaenophorus	Baird	1853
Triaenophorus	Molin	1858
Triaenophorus	Molin	1861
Triaenophorus	Diesing	1863
Triaenophorus	Olsson	1867
Triaenophorus	Lönnberg	1889
Triaenophorus	Olsson	1893
Triaenophorus	Lühe	1899
Triaenophorus	Lühe	1899
Triaenophorus	Braun	1900
Triaenophorus	Lühe	1900
Tricuspidaria	Stiles and Hassall	1902
Triaenophorus	Lühe	1910

Scolex armed with four three-pointed hooks, never replaced by a pseudoscolex. External segmentation completely absent. Longitudinal nerves dorsal to the cirrus-sac and vagina, close to the lateral borders. Testes between the nerve strands only, filling up the whole medullary parenchyma so far as this is not occupied by other organs; a testis-free middle field is quite as infrequently present as a pronounced dorsal layer of the testes. Coiling of the vas deferens in its proximal almost medially situated part, that portion passing distad to the cirrus-sac only very slightly coiled. Vitelline follicles form a continuous mantle between the subcuticula and the longitudinal musculature, which is broken only at the places where the genital ducts open. Ovary, approaching the lateral border bearing the genital openings, lies on the ventral transverse musculature, yet individual ovarian tubules extend partly thruout the whole medulla. Shell-gland just as infrequently median as the ovary lying behind it, also usually approaching the dorsal surface somewhat. First portion of the uterus only a weakly coiled canal (uterine duct) which passes thru the proglottis transversely and leads into a large single cavity (uterus-sac) which lies not exceptionally ahead of, but yet partly near the ovary, and usually not median but away from the margin bearing the genital openings. The latter also applies naturally to the uterus-openings which breaks thru later. Eggs thick-shelled, operculate.

Type species: *T. nodulosa* (Pallas 1781) Rudolphi 1793.

As indicated in the above synonymy the name Triaenophorus has absolute page priority altho Stiles and Hassall (1902:22) have contended that Rudolphi should not have changed the name of the genus in 1819 from Tricuspidaria to Triaenaphorus again, after having used it in connection with the specific description in 1810. The change has become so universally established in the literature that it does not seem justifiable to revert to the name Tricuspidaria which is known to only a comparatively small group of zoologists.

TRIAENOPHORUS sp. larv.

[Figs. 12-18]

Since all of the material at hand was larval, not even the earliest traces of the reproductive rudiments showing in toto preparations of the largest specimens, it was, of course, impossible to determine the species with certainty.

Two types of scolices are present, however, and these agree with the descriptions of the organ given by various authors for *T. nodulosus* (Pallas) and by Olsson (1893:20) and Fuhrmann (1910:88) in particular, for *T. robustus* Olsson. It will be seen also in the table below that these two forms are found respectively encysted in the liver, on the visceral organs, or in the wall of the stomach, and encysted in the muscles or free in the intestine of the hosts—in the latter case so firmly attached to the wall as to be deeply imbedded, the mucosa forming a protruding collar around the worm—the only exception being those from the intestines of *Esox masquinongy* and *Stizostedion vitreum* (*vide infra*). Olsson pointed out that these two species can be readily differentiated from each other on account of the situations in which they undergo their development. Whereas the larvae of *T. nodulosus* are found generally

within cysts in the liver of the intermediate hosts, as recorded by a number of writers, those of *T. robustus* are constantly encysted in large numbers in the flesh—Olsson having found them in *Coregonus albula* and *C. lavaretus*, Luther (1909:58) in *C. albula*, and Fuhrmann in the "brochet" (? *Esox lucius*).

The scolex of the *robustus* type (Figs. 12 and 13) is, as described by Olsson, in the form of a truncated rectangular pyramid, that part immediately behind the terminal disc being considerably constricted and more nearly elliptical in transverse section. As stated by Fuhrmann, "La limite posterieure du scolex de *T. robustus* est nettement marquée et les deux bothrias, l'un dorsal l'autre ventral, son très profonds. . . . " This delimitation of the scolex is emphasized by the fact that immediately behind the posterior border of the bothria the dorsal and ventral surfaces of the body of the larva are distinctly concave as are also the lateral surfaces, quite diagrammatically, in fact, as shown in the figures. These concavities extend farther back for a few millimeters and then gradually flatten out and pass insensibly into the convexities which together form the elliptical outline of the cross-section of the middle of the larva. And it should be emphasized that this was found to be a constant feature of all the material studied and not simply due to any possible local collapsing during dehydration. Altho, as shown in the table, the measurements of the whole scolex are much smaller than those given by Fuhrmann, as might be expected it is chiefly the structure and size of the trident of hooks that leads the writer to consider this type of larva to belong to *T. robustus*. Figure 14 of one of these compares very favorably with those shown in Olsson's figures 31 and 32 and Fuhrmann's figure 2, while the measurements (see table) quite agree with those given by the latter. The base of the trident is comparatively long or deep (in the sagittal direction), hence the specific name according to Olsson, while not only the full length of the larger hooks but also a good deal of the median ones project thru the cuticula as the functional tips. In figure 14, which is from an alcoholic specimen, these are seen to be darker than the basal piece. The following measurements are given for comparison with Fuhrmann's of adult specimens, which are placed alongside, the data in parentheses being of the opposite trident on the same surface of the scolex in question:

Host	*Esox lucius*		*Leucichthys artedi*		After Furmann
Length	147.5mm.	123.0m.	183.0mm.	47.0mm.	310-370mm.
Breadth (maximum)	1.07	1.16	0.98	1.10	4.00-4.50
Length of scolex	0.98	0.96	1.02	1.12	1.14-1.50
Breadth of term. disc.	0.77	0.83	0.84	0.84	0.95
Breadth of scolex posterly	1.05	1.07	1.30	1.08	1.40-1.50

Host	*Esolucius*		*Leucichthes artedi*		After Fuhrmann
Width of trident	0.31(0.30)	0.30(0.30)	0.32	0.28	0.29-0.32
Length, mediad	0.25(0.24)	0.23(0.23)	0.27	0.22	0.24-0.28
Length, externally	0.18(0.18)	0.16(0.18)	0.24	0.18	0.18-0.20
Measured in	Oil of wintergreen		Alcohol		

Olsson spoke of the larva of *T. robustus* being provided with a narrower cylindrical "cauda" as in certain Tetrarhynchus larvae, and gave the length of one as 120mm., while the anterior portion was approximately 60mm. long. Such structures were seen posteriorly in many of the larger larvae at hand but their lengths and degrees of distinction from the fore-body varied considerably. A medium large one, in a lot from *Esox lucius*, for instance, had these measurements: Length of anterior portion, 48mm., of cauda 24, of scolex 1.16; width of forebody 0.66, of cauda 0.37 (3:1—Olsson). The specimen from *Leucichthys artedi* dealt with in the third column of the above table possessed a cauda 110mm. in length, while that treated in the fourth column had no posterior appendage at all. As for its anatomical structure this organ is characterized by very poorly developed cuticula and musculature, and a very loose or open parenchymatous mesh-work.

As may be seen by reference to the host record given below the specimens taken from *Leucichthys artedi* were the only ones belonging to this type of larva which were found encysted. From 26 specimens of the host examined by the writer, 14 cysts, each containing a single larva, were taken. Each fish harbored one or two cysts, but one contained four. The cysts themselves are from 15 to 45mm. in length and 2 to 3mm. in diameter, and cylindrical in shape, with bluntly pointed ends. They are often attentuated at one end to such an extent that at first sight they appear to be terminated by a mere thread. This is found, however, on closer examination to be hollow and to place a more distal, but somewhat smaller portion of the cyst in communication with the main body. In situ these cysts are located constantly in the myocommata of the dorsal musculature of the host, from a short distance back of the dorsal fin to close behind the skull, and with their longitudinal axes directed downward, inward, and forward towards the spinal column, or, indeed as was seen in one case, actually towards the dorsal aorta. Often they are found doubled on themselves in a V-shaped manner. Their translucent white or somewhat opalescent color is due to the contents, which besides the worm coiled on itself several times consists of a caseous substance, showing thru the thin wall.

On the other hand, the other type of larva which is considered by the writer to belong to *T. nodulosus*, is characterized by a much shorter, narrower body, smaller at irregular intervals owing to differences of contraction, whence the specific name, and by a quite different scolex provided with the well-

known form of trident (Figs. 15 to 16). While the latter and the scolex as seen in surficial view agree in essentials with the descriptions and figures given by various authors, e.g., Rudolphi (1810:32, Tab. IX, Figs. 6-11), Wagener (1854: 26, Tab. 2, Figs. 17-21), Olsson (1893:20, Figs. 28-32) and Fuhrmann (1910:86, Fig. 1), it cannot be said of the material studied that, as stated by the last writer, ". . . chez *T. nodulosus* on ne peut voir aucune limite entre le scolex et le cou du Bothriocephale. . . ." For in lateral view (Fig. 16) the bothria are distinctly separated from the beginning of the body, which is, as just mentioned, not nearly so apparent in surficial view. As shown in figure 15, the middle hook of the trident scarcely protrudes thru the cuticula, since it is the root for muscular attachment. The upper median hook (cf. Wagener) which does protrude in the adult is evidently not yet developed (Figs. 17 and 18). For a short distance behind the scolex the body is somewhat rectangular in cross-section, the sides of the rectangle being, however, slightly convex and not concave as in the *robustus* type, and hence not so very different from the cross-section of the body farther back. But the material contained in the lot from the intestine of *Esox masquinongy* does not strictly answer this description since the body just behind the scolex is slightly concave on all sides. Otherwise the specimens are distinctly of the *nodulosus* type. It should be mentioned, too, that one of this lot showed a very short but distinct caudal piece; but this with the general stout appearance of all of them may be accounted for by the possibility that they have reached the intestine of one of their final hosts and continued their development. Likewise a few of the specimens of the lots from the "white bass" and *Stizostedion canadense* were provided with short caudal appendages. The smallest example of this type and of all the material, for that matter, at hand was that from *Micropterus dolomieu* of the accompanying table. Altho it is only a little over two and a half millimeters in length, its posterior end shows that a portion, perhaps a caudal piece, has been torn away. The following table gives measurements of a number of specimens of the *nodulosus* type, similar to those given above for the *robustus* type, with Fuhrmann's data for comparison:

Host	*Catostomus commersonii*	*Esox masquinongy*	*Micropterus dolomieu*		After Fuhrmann
Length	Piece	Piece	Piece	2.68	120-180mm.
Breadth at middle	0.61	0.37	0.42	0.30	2.50-4.00
Length of scolex	0.92	0.63	0.55	0.55	0.95
Width term. disc.	0.42	0.35	0.37	0.31	0.37-0.47
Width of scolex posteriorly	0.64	0.37	0.37	0.26	0.57-0.60
Width of trident	0.19	0.15	0.15	0.13	0.125
Width of trident medially	0.14	0.13	0.11	0.14	0.073
Width of trident externally	1.11	0.09	0.08	0.10	0.062
Measured in	Oil of wintergreen				

It will be noticed that in spite of the fact that all of the measurements of the tridents are larger than those given by Fuhrmann, they are considerably smaller than those of the other type.

Finally, altho no specimens of either type of larva so young that the hooks had not yet developed were met with, those from the intestine of *Stizostedion vitreum* were provided with only very small tridents of the *nodulosus* form, the bases of which were not yet well developed. The whole scolices were a sort of compromise between the two types in shape but of the *nodulosus* type as regards size, as shown in the following measurements: Length, 12mm.; width at middle, 0.64; length of scolex, 0.87; width of terminal disc, 0.64; same of scolex posteriorly, 0.80; width of trident, 0.14, length medially, 0.07, externally, 0.05. Altho these specimens would seem to represent an intermediate stage between the two types of scolex so far as the general shape is concerned, the writer was inclined to consider them as belonging to the *nodulosus* type; yet it must be said that smaller scolices, e.g., those from *M. dolomieu* in the table, have considerably larger hooks.

On the whole, then, the bulk of the evidence given here tends to show that here in America there are probably two species, very closely related to, if not identical with, the European *T. nodulosus* and *T. robustus* which have been clearly distinguished by Fuhrmann (1910) and also recognized by Lühe (1910: 23). However, no adults have as yet been reported for this continent, so far as the writer is aware.

The material studied is here listed as a host record also:

LOT	HOST	LOCATION	LOCALITY	COLLECTOR
Type *robustus*.				
36	*Esox lucius*	Intestine	Flat Rock L. Muskoka, Ont.	Cooper
36a, 36b, 36c	*Esox lucius*	Intestine	Go-Home R., Muskoka, Ont.	Cooper
161, 163, 183,	*Esox lucius*	Intestine	Go-Home Bay,	Cooper
162	*Lota maculosa*	Intestine	Off Giant's Tomb Id., Georgian Bay, Lake Huron	Cooper
15.47	"Lake Herring"	? Intestine	Lake Superior	H. B. Ward
186a, 194b, 195a, 196a, 197a, 25f, 25g	*Leucichthys artedi*	Muscles	Douglas Lake, Michigan	G. R. LaRue
331, 333, 336, 337	*Leucichthys artedi*	Muscles	Douglas Lake, Michigan	Cooper

Type *nodulosus*:	Host	Location	Locality	Collector
71	*Perca flavescens*	In liver	St. Lawrence R., Iroquois, Ont.	Cooper
151, 188	*Micropterus dolomieu*	In viscera	Go-Home Bay	Cooper
195	*Catostomus commersonii*	?	Georgian Bay	Cooper
Eh3b	*Notropis delicatus*	?	Charlevoix, Mich.	H. B. Ward
10213 .	"White Bass"	Liver	?	H. B. Ward
N. S. 28a	*Stizostedion canadense*	Stomach wall	New Baltimore, Michigan	H. B. Ward
40	*S. vitreum*	Intestine	Flat Rock L.	Cooper
35	*Esox masquinongy*	Intestine	Go-Home R.	Cooper

FISTULICOLA Lühe 1899

Taenia (part.)	Pallas	1781
Bothriocephalus (part.)	Rudolphi	1819
Bothriocephalus (part.)	Leuckart	1819
Bothriocephalus (part.)	Dujardin	1845
Dibothrium (part.)	Diesing	1850
Dibothrium (part.)	Diesing	1863
Bothriocephalus (part.)	Linstow	1878
Bothriocephalus (part.)	Carus	1885
Bothriocephalus (part.)	Matz	1892
Bothriotaenia (part.)	Ariola	1896
Bothriotaenia (part.)	Riggenbach	1896
Fistulicola	Lühe	1899
Bothriotaenia (part.)	Ariola	1900
Fistulicola	Braun	1900
Fistulicola	Lühe	1902

Scolex unarmed, arrow-shaped (since the posterior borders of the surficial bothria protrude comparatively strongly), may be replaced by a pseudoscolex. Neck absent. Chain of proglottides very thick, so that transections may be nearly circular. Segmentation strongly expressed, the individual proglottides very short with leaf-like, free lateral portions. Longitudinal nerves strongly approaching the lateral borders; individual testes, however, are also present outside of them. Pronounced coiling of the vas deferens in its proximal portion; the distal part near the cirrus-sac only weakly coiled. Receptaculum seminis comparatively small and obscure, but at the same time sharply set off from the narrow terminal portion of the vagina (the spermiduct), which in contrast with the Ligulinae, Dibothriocephalinae and Cyathocephalinae is comparatively long. Ovary and shell-gland, near the corresponding parts of the female ducts, are, in consequence of the shortness of the proglottides and the strong development of the uterus, forced away from the position which they usually occupy in the Dibothriocephalidae, or towards the ventral surface or the margin bearing the genital openings. Vitelline follicles extraordinarily numerous, not confined to two lateral fields, but in the form of a ring, outside of the longitudinal musculature in the free lateral leaf-like portions of the proglottides. Uterus a comparatively wide, strongly coiled canal; that portion near its opening very muscular. The eggs pass thru their embryonic development (at least for the most part) in the uterus.

Type species: *F. plicatus* (Rudolphi).

FISTULICOLA PLICATUS (Rudolphi 1819)

1781	*Taenia haeruca*	Pallas	1781 : 108
1790	*Echinorhynchus xiphiae*	Gmelin	1790 : 3047
1803	*Echinorhynchus xiphiae*	Zeder	1803 : 162
1809	*Echinorhynchus xiphiae*	Rudolphi	1809 : 308
1816	*Echinorhynchus xiphiae*	Lamarck	1816 : 582
1819	*Bothriocephalus plicatus*	Rudolphi	1819 : 136, 470
1819	*Bothriocephalus truncatus*	Leuckart	1819 : 37
1829	*Bothriocephalus plicatus*	Creplin	1829 : 87
1839	*Bothriocephalus plicatus*	Creplin	1839 : 297
1845	*Bothriocephalus plicatus*	Dujardin	1845 : 614
1850	*Dibothrium plicatum*	Diesing	1850 : 591
1854	*Dibothrium plicatum*	Wagener	1854 : 71
1863	*Dibothrium plicatum*	Diesing	1863 : 243
1869	*Bothriocephalus plicatus*	Cobbold	1869 : 71
1871	*Dibothrium plicatum*	Van Beneden	1871 : 36
1878	*Bothriocephalus plicatus*	Linstow	1878 : 218
1885	*Bothriocephalus plicatus*	Carus	1885 : 120
1890	*Dibothrium plicatum*	Linton	1890 : 746
1892	*Bothriocephalus plicatus*	Matz	1892 : 117
1896	*Bothriotaenia plicata*	Ariola	1896
1896	*Bothriotaenia plicata*	Ariola	1896 : 280
1896	*Bothriotaenia plicata*	Riggenbach	1896 : 223
1898	*Dibothrium plicatum*	Linton	1898 : 430
1898	*Bothriocephalus plicatus*	Muehling	1898 : 36
1899	*Fistulicola plicatus*	Lühe	1899 : 37
1899	*Fistulicola plicatus*	Lühe	1899a
1900	*Bothriotaenia plicata*	Ariola	1900 : 437
1900	*Fistulicola plicatus*	Braun	1900 : 1695
1900	*Fistulicola plicatus*	Lühe	1900a : 98
1901	*Dibothrium plicatum*	Linton	1901 : 267
1901	*Dibothrium plicatum*	Linton	1901a: 412, 448
1902	*Fistulicola plicatus*	Lühe	1902a : 321, 324, 329
1903	*Bothriotaenia plicata*	Barbagallo and Drago	1903 : 412
1905	*Fistulicola plicata*	Spengel	1905 : 273
1914	*Fistulicola plicatus*	Rudin	1914 : 321

Specific diagnosis: With the characters of the genus. Large cestodes with maximum length, breadth and thickness of 250 (about 60 when contracted), 20 and 5mm. respectively. Scolex somewhat orbicular, 2mm. long, 1.3 wide and 1.8 thick; present only in young strobilas which are free in the intestine of the host; later it becomes modified as does a considerable portion of the anterior end of the strobila to form a pseudoscolex which is found deeply imbedded in the wall of the host's rectum or completely piercing it. Segmentation begins immediately behind the scolex or pseudoscolex. First and middle segments very short and broad, with prominent posterior and wavy borders; posterior joints 0.4, 7 and 3mm. in length, breadth and thickness respectively, funnel-shaped with prominent posterior borders which occupy two-thirds or more of the transverse diameter; terminal segments relatively much longer, narrower and conical in shape, their posterior margins very thin and leaf-like.

Cuticula 10μ in thickness, subcuticula 50 to 55μ. Calcareous bodies 15 to 25 by 10 to 15μ in dimensions, mostly outside of the longitudinal muscles. Latter not in bundles but distributed thruout the cortical parenchyma, separated into outer and inner groups only in young proglottides. Transverse and sagittal fibres likewise diffuse, former more numerous, however, just outside of the medulla. Chief nerve strand 45μ in diameter, situated far towards the margin of the strobila on each side, passing dorsal to the cirrus-sac and vagina. Excretory system in the form of a plexus of vessels ramifying thruout the whole of the medulla, of which one just within the nerve on each side is small in caliber but provided with thick muscular walls.

No genital cloaca, but the vagina opens immediately behind the cirrus-sac, the outer half of which forms a protruding papilla from 0.4 to 0.6mm. in length and with a marked constriction at its base. Uterus opening about half-way between the median line and the margin bearing the other genital apertures, and on the free posterior portion of the proglottis.

Testes polyhedral in shape; closely arranged, forming a dorsal layer continuous from side to side but discontinuous from proglottis to proglottis; 90 to 130, 55 to 75 and 90 to 185μ, in length, breadth and thickness respectively; quite numerous outside of the nerve strands, at least 200 to each proglottis. Vas deferens strongly coiled and compact in the median line, less coiled laterally; median and distal portions lined with ciliated epithelium; no special enlargement at any point in its course to form a vesicula seminalis. Cirrus-sac 0.5 to 0.7mm. in length by 0.2 to 0.4 in maximum diameter; outer half or more forming the pyriform, protruding cirrus, the cuticula over which is deeply cleft. This functional cirrus may be augmented in length by the further evagination of the cirrus proper from the papillary portion of the organ.

Immediately within its opening the vagina is surrounded by a sphincter, 0.2mm. in diameter, which is followed by a slight enlargement of the lumen to a diameter of 60μ; much coiled laterally but straighter medially; 20μ in diameter at the middle of its course; spermiduct inconspicuous. Ovary irregular in shape, median in position and considerably depressed, 0.7mm. in transverse diameter by 0.1 in thickness, isthmus prominent, ova from same 25μ in maximum diameter. Oocapt 25μ in diameter, oviduct 40μ. Vitelline reservoir 75μ in diameter when filled with vitelline material. Vitelline follicles irregular in shape, very numerous; discontinuous from proglottis to proglottis, but form a continuous layer laterally and dorsoventrally in the free posterior borders of the segments. Shell-gland inconspicuous. Uterus in gravid joints occupies almost the whole of the medulla; 0.16 to 0.20mm. in diameter at its middle; the terminal portion quite muscular, and sharply separated from the duct immediately before it, 0.2 to 0.3mm. in length by 0.10 to 0.15 in diameter; opening irregular in shape and size.

Eggs thick-shelled (2 to 4μ) with dimensions of 0.09 to 0.10 by 0.05 to 0.06mm.

Habitat: In the rectum—less frequently in the stomach and anterior portion of the intestine—of the host.

HOST	LOCALITY	COLLECTOR	AUTHORITY
Xiphias gladius (type host)	Pisa	Redi	Rudolphi 1809 : 309
Xiphias gladius	Baltic Sea	Rudolphi	Rudolphi 1819 : 471
Xiphias gladius	Ticini	Spedalieri	Diesing 1850 : 591
Xiphias gladius		Kais.-König. Nat'l Kab.	Leuckart 1819 : 37
Xiphias gladius		. .. .	Dujardin 1845 : 614
Xiphias gladius	Gryphswald	Rosenthal	Diesing 1850 : 591
Xiphias gladius		M. C. V.	Diesing 1850 : 591
Xiphias gladius	Lynn, Norfolk, England	Cobbold	Cobbold 1869 : 71
Xiphias gladius	Coast of Norway	Olsson	Beneden 1871 : 36
Xiphias gladius	Escaut		Beneden 1871 : 36
Xiphias gladius	Holland		Beneden 1871 : 36
Xiphias gladius	Firth of Forth, Edinburgh		Beneden 1871 : 36
Xiphias gladius	Nizza	Wagener	Carus 1885 : 120
Xiphias gladius	Martha's Vineyard, Mass.	Linton	Linton 1890 · 750
Xiphias gladius	Genova	Ariola	Ariola 1896a · 121
Xiphias gladius		U. S National Museum	Linton 1898 : 430
Xiphias gladius	Konigsberg	Braun	Muehling 1898 : 36
Xiphias gladius	Siracusa	Condorelli	Ariola 1900 : 438
Xiphias gladius	Naples	Ariola	Ariola 1900 : 438
Xiphias gladius	Casco Bay, Me.	U. S. National Museum	Linton 1901a : 448
Xiphias gladius	Woods Hole, Mass	Linton	Linton 1901a : 448
Xiphias gladius	Messina, Italy	Barbagallo and Drago	Barbagallo and Drago 1903 : 412
Xiphias gladius	Messina, Italy	Janicki	Rudin 1914 : 321
Xiphias gladius	Woods Hole, Mass	H. B. Ward	Cooper (the present paper)
"Sunfish" (Mola ?)	Woods Hole, Mass.	V. N. Edwards	Cooper (the present paper)

This species has been so well described by Linton (1890:746), Ariola (1896a) and Lühe (1899a, 1900a) that little need be added. The writer would like to point out, however, that as regards a few details the material studied did not agree with the descriptions given by these writers.

After referring to the fact that the testes are not arranged in two lateral fields but form a continuous dorsal layer and the further fact that, contrary to Ariola's statement, they are to be found evidently functioning in gravid segments, Lühe (1899a:709) stated that "Ihre Anzahl ('pochi' nach Ariola, 'zahlreich' nach Loennberg) beträgt ca. 50 pro Proglottis." In the sections made they were found to be about 200 in number for each proglottis, and separated from those of the segments ahead and behind by aggregations of transverse and sagittal muscles which are, however, so narrow as to give the closely

crowded organs the appearance at first sight of being continuous thruout the strobila.

The vagina was described by Lühe (1900a:68) as being provided with no cuticular lining within the enlargement just beyond the sphincter, but in the sections made by the writer the cuticula could be followed for about half the length of the whole duct. Peripherally as in the case of that lining the terminal enlargements, it was seen to be thrown into prominent longitudinal folds which in transections were in many places fused together so as to divide the lumen into several passages. Farther on these folds become less pronounced and fused, while their borders towards the center of the lumen gradually become broken up into pseudocilia. Beyond the middle of the course of the duct these pseudocilia seem to pass insensibly into the cilia of the proximal region, while the cuticula is likewise strictly continuous with the nucleated epithelium, there being no distinct region, let alone line of demarcation in either case. It would appear, then, that what are apparently true cilia in the proximal portion of the duct are merely modified cuticular pseudocilia; or from the standpoint of development that the latter, as well as the more peripheral ridges, are formed by the gradual fusion of the former from within outwards. But since this view needs considerable ontogenetic evidence for its support, it must remain for the present, at least, a mere suggestion of possibility.

Otherwise the material studied, which was quite fragmentary, corresponded with the descriptions given by the various authors of the species found on the European side of the Atlantic Ocean, as was brought out by Linton (1890) for the general features. It consisted of No. 13.46 of the Collection of the University of Illinois from the stomach wall of *Xiphias gladius*, and one specimen taken by Mr. V. N. Edwards from a "Sunfish" (? *Mola mola*) at the Woods Hole Laboratory of the U. S. Bureau of Fisheries.

PTYCHOBOTHRIIDAE Lühe 1902

Scolex unarmed, with two separate and more or less strongly developed bothria, or exceptionally replaced by a pseudoscolex. Neck absent. External segmentation never absent, but frequently incomplete or obliterated thru secondary foldings. Genital organs numerous, but only single in each proglottis. Both surfaces of the chain of proglottides, apart from the genital openings similar. Cirrus unarmed, with cleft cuticula. Opening of cirrus and vagina behind the uterus opening, surficial or marginal, in the first case on the opposite surface to the uterus-opening and almost median. No muscular bulb at the inner end of the cirrus-sac. Receptaculum seminis, when present, has the form of a small blind sac situated at the inner end of the vagina. Ovary and shell-gland median. Testes in two lateral fields. Uterus never taking the rosette shape, but usually forming a capacious undivided uterus-sac. Eggs thin-shelled, without opercula; embryonic development in the uterus, and in consequence of exhaustive production of eggs (but dependent on the time of year in the case of many species) all the eggs of the whole tapeworm are at the same stage of development.

Sexually mature in the intestine of fishes; larval condition unknown.

In his first diagnosis of the family Lühe (1902a:326) emphasized the similarity of both surfaces of the strobila (in contradistinction to conditions in the Acanthophallidae), the unarmed cirrus with cleft cuticula, the peculiar cecal receptaculum seminis and the absence of opercula in the eggs, but described the uterus as follows: "Uterus nie die sogenannte Rosettenform annehmend, wohl aber in der Regel eine geräumige Uterushöhle bildend, welche die übrigen Genitalorgane, ohne dass freilich deren Rückbildung eintritt, buchstäblich an die Wand drängen kann, indem die ganze Proglottis in reifen Proglottiden vielfach als ein einziger sackförmiger Eibehälter mit verhältnismässig sehr dünnen Wandungen erscheint." The uterus of Haplobothrium answers this description in that it is divided into a uterus-sac and uterine duct; but the remaining reproductive organs are distinctly diphyllobothriidian in their nature. Consequently, in order to differentiate more clearly the two families, Ptychobothriidae and Diphyllobothriidae, and especially since the genus Haplobothrium presents difficulties in this connection, it is necessary to know the developmental relationships between the uterine duct and the uterus-sac in those genera in which they appear. Up to the present no adequate descriptions of the latter have been published, so that here will be given the observations on the development of the uterus to which reference was made above (p. 16), where the conditions in Haplobothrium and Marsipometra were discussed.

In *Bothriocephalus scorpii* the lumen of the uterus-sac appears suddenly and with a diameter of 90μ, the rudiment ahead showing as yet no signs of forming a cavity. This enlargement is situated at first, however, in the cortical parenchyma and among the longitudinal muscles, only the inner tip of the

structure in transections going into the medulla. Just within the inner transverse muscles this inner portion of the sac is joined by the uterine duct which with a diameter of 30μ elsewhere is here only 8μ in diameter. Furthermore, in the genital rudiment of the next proglottis ahead there is a distinct demarcation between the aggregagion of nuclei that will form the sac and the axial rudiment of the uterine duct. The same separation of sac and duct with the narrowing of the latter just before entering the former is present in the following segments even where the first eggs are to be seen in the lumen. Thus the eggs must have passed this narrowed region which is a great deal smaller than their diameters. Still farther back where the lumen is about 165μ in diameter there can be seen not only the situation of the sac in the cortex and among the longitudinal muscles, projecting as yet only a short distance into the medulla—altho here the bundles of muscles are deflected peripherally—but also the separation of the two parts by a narrow neck only 10μ in diameter. *B. cuspidatus* shows the same distinct separation of the uterine duct and uterus-sac in the proglottides where there are already a few eggs in the latter. In *Clestobothrium crassiceps* conditions were found to be quite the same. When the lumen of the sac attains dimensions of about 60 by 35μ and is lined with an epithelium which takes the counterstain more like a cuticula but shows nuclei on its surface towards the lumen, the uterine duct opens into it with a distinct reduction in diameter. The epithelia of the two are, however, quite similar and continuous, the nuclei being located in a similar manner in both. Proglottides ahead show that the sac is formed by an enlargement of the end of the duct, which takes place first in that region passing thru the cortex quite as in Bothriocephalus.

Thus it is seen that the uterus sac of this family is quite different from the functional enlargement of the uterus of the Diphyllobothriidae, with the exception of that of Haplobothrium, since at all stages in its development it is sharply separated from the uterine duct. But as it was not so much this exact separation of the two portions as the constant presence of an "Uterushöhle" in this family and its absence in the other, where the "Rosettenform" is more common, that was emphasized by Lühe, and since the structure in Haplobothrium is distinctly ptychobothriidian in character, the functional enlargement of the uterus cannot now be considered to be of such systematic importance as was formerly believed.

PTYCHOBOTHRIINAE Lühe 1899

Scolex with two surficial sucking grooves, which may be modified by considerable growth together of their free edges. Genital openings surficial, those of the cirrus and vagina dorsal, that of the uterus ventral and ahead of the other two. Vas deferens strongly coiled, dorsal. Ovary ventral; shell-gland dorsal. Vitelline follicles usually in two lateral fields in the cortical or medullary parenchyma. Testes completely filling the medulla, mostly marginal to the longitudinal nerves which are well towards the median line.

Occurrence: Exclusively in fishes.

Type genus: Bothriocephalus (Rud.) Lühe.

The above diagnosis lacks the words "seldom armed" after "scolex" which appear in Lühe's latest (1910:24) characterization not only of this subfamily but of the family, because they do not appear in his earlier papers, (1899:41 and 1902a:336, respectively) nor does there seem to the writer to be any occasion for their use.

BOTHRIOCEPHALUS Rud. 1808, e. p. Lühe 1899, e. p.

Taenia (part.)	Auctorum	
Rhytelminthus (part.)	Zeder	1800
Alyselminthus (part.)	Zeder	1800
Rhytis (part.)	Zeder	1803
Bothriocephalus (part.)	Rudolphi	1809
Bothriocephalus (part.)	Rudolphi	1819
Dibothrius (part.)	Rudolphi	1819
Bothriocephalus (part.)	Leuckart	1819
Bothriocephalus (part.)	Dujardin	1845
Dibothrium (part.)	Diesing	1850
Bothriocephalus (part.)	Baird	1853
Dibothrium (part.)	Molin	1861
Dibothrium (part.)	Diesing	1863
Bothriocephalus (part.)	Carus	1885
Bothriocephalus (part.)	Matz	1892
Bothriocephalus (part.)	Ariola	1896
Bothriocephalus s. str.	Lühe	1899
Bothriocephalus (part.)	Ariola	1900
Bothriocephalus s. str.	Braun	1900
Bothriocephalus s. str.	Lühe	1910

Scolex elongated, with two only weakly developed sucking grooves. External segmentation well developed; between two consecutive genital segments there is always present a saw-tooth notching of the lateral border, yet a corresponding transverse furrow on both surfaces is sometimes lacking. Vitelline follicles in the cortical parenchyma, continuous from proglottis to proglottis, as are the testes. Receptaculum seminis absent. Beginning of the uterus a winding canal (uterine duct) which opens into a large nearly spherical cavity (uterus-sac or uterus s. str.). Uterus opening approximately median, as is the dorsal genital opening.

Type species: *Bothriocephalus scorpii* (Müller 1776)

BOTHRIOCEPHALUS SCORPII (Müller 1776)

[Figs. 21, 22, 55-57, 59-61, 71, 84, 95, 105]

1722	*Vermis multimembris rhombi*	Leeuwenhoek	1722 : 402
1776	*Taenia scorpii*	Müller	1776 : 219
1780	*Taenia scorpii*	Müller	1780 : 179
1780	*Taenia scorpii* (part.)	Fabricius	1780 : 319
1786	*Taenia scorpii*	Batsch	1786 : 235
1788	*Taenia scorpii*	Müller	1788 : 5-6
1788	*Taenia scorpii*	Schrank	1788 : 48
1790	*Taenia scorpii*	Gmelin	1790 : 3078
1799	*Taenia scorpii*	Ratke	1799 : 68
1800	*Alyselminthus bipunctatus*	Zeder	1800 : 236
1802	*Taenia punctata*	Rudolphi	1802 : 109-110
1802	*Taenia scorpii*	Bosc	1802 : 307
1803	*Rhytis bipunctata*	Zeder	1803 : 296
1810	*Bothriocephalus punctatus*	Rudolphi	1810 : 50
1819	*Bothriocephalus punctatus*	Rudolphi	1819 : 138
1819	*Bothriocephalus punctatus*	Leuckart	1819 : 40
1844	*Bothriocephalus punctatus*	Bellingham	1844 : 254
1845	*Bothriocephalus punctatus*	Dujardin	1845 : 617
1850	*Bothriocephalus punctatus*	van Beneden	1850 : 160
1850	*Dibothrium punctatum*	Diesing	1850 : 593
1853	*Bothriocephalus punctatus*	Baird	1853 : 89
1855	*Dibothrium punctatum*	Leidy	1855 : 444
1856	*Dibothrium punctatum*	Leidy	1856 : 46
1858	*Bothriocephalus punctatus*	Cobbold	1858 : 157
1858	*Dibothrium punctatum*	Molin	1858 : 134
1861	*Dibothrium punctatum*	Molin	1861 : 235
1863	*Dibothrium punctatum*	Diesing	1863 : 240
1867	*Bothriocephalus punctatus*	Olsson	1867 : 14, 55
1878	*Bothriocephalus punctatus*	Linstow	1878 : 237
1885	*Bothriocephalus punctatus*	Carus	1885 : 120
1889	*Bothriocephalus punctatus forma bubalidis*	Loennberg	1889 : 32
1890	*Dibothrium punctatum*	Linton	1890 : 731
1891	*Bothriocephalus punctatus*	Loennberg	1891 : 51
1892	*Bothriocephalus punctatus*	Matz	1892 : 105
1893	*Bothriocephalus punctatus forma motellae*	Loennberg	1893 : 13
1893	*Bothriocephalus punctatus*	Olsson	1893 : 16
1898	*Dibothrium punctatum*	Linton	1898 : 430
1899	*Bothriocephalus bipunctatus*	Lühe	1899 : 43
1900	*Bothriocephalus punctatus*	Ariola	1900 : 394
1900	*Bothriocephalus bipunctatus*	Braun	1900 : 1691
1902	*Bothriocephalus bipunctatus*	Fuhrmann	1902 : 446
1902	*Bothriocephalus punctatus forma punctatus vel typica*	Schneider	1902a : 14
1902	*Bothriocephalus punctatus forma rhombi*	Schneider	1902a : 15
1902	*Bothriocephalus punctatus forma cotti-quadricornis* [mihi]	Schneider	1903 : 75
1910	*Bothriocephalus bipunctatus*	Lühe	1910 : 25
1917	*Bothriocephalus scorpii*	Cooper	1917 : 37

Specific diagnosis: With the characters of the genus. Large cestodes, up to 950mm. long by 6mm. wide. Scolex, large, elongate, with prominent

terminal disc, widest anteriorly; length 1.0 to 3.5mm., breadth 0.3 to 0.5. Bothria long and narrow, shallow posteriorly. First segments subcuneate with weakly prominent posterior borders, longer than broad. Middle and posterior segments much depressed, former very short and broad, latter relatively less so and grouped in twos or threes; lateral borders crenulate. Ripe proglottides 2 to 4mm. wide by 0.2 by 0.8 long. Strobila usually incomplete posteriorly.

Cuticula 5μ in thickness. Calcareous bodies 13μ in diameter. Inner longitudinal muscles in fascicles. Six chief longitudinal excretory vessels.

Opening of the genital cloaca at the bottom of a dorsal median longitudinal depression running thruout mature segments, on a low papilla in each proglottis and half-way between the anterior and posterior borders. Vaginal opening immediately behind that of cirrus. Distinct ductus hermaphroditicus present.

Testes subspherical, 35 to 70μ in diameter and 30 to 60 in each segment. Vas deferens a compact mass lateral to cirrus-sac and opposite the uterine tube, 0.18 by 0.10mm. Cirrus-sac at right angles to dorsal surface, 115 by 120 by 75 to 80μ, extending only a short distance into the medulla; thick layer of nuclei within its wall. Cirrus proper, not protruded, 65 by 15μ.

Ovary compact, tubulolobular, 0.33mm. wide by 0.15 long where uterus-sac is not greatly distended. Isthmus only ventral. Oocapt 35μ in diameter. Vitelline follicles in two lateral weakly united fields on each surface, 350 to 540 in number, 35 to 55μ in diameter; vitelline reservoir small. Shell-gland large, 115μ wide by 85μ deep, median, close behind cirrus-sac. Uterine duct voluminous on both sides of the median line, closely applied to ovary behind. Uterus-sac spherical to flattened anteroposteriorly, occupies one-sixth of transverse diameter of proglottis, alternating irregularly from side to side, or often quite median. Opening in middle of sac, ventral and well forward, formed by the rupture of a distinct membrane.

Eggs, 66 to 80μ in length by 43 to 45μ in diameter, without opercula, forming dark brown maculations in ripe proglottides as they show thru the walls of the uterus-sacs.

Habitat: In the intestine of the host.

HOST	LOCALITY	COLLECTOR	AUTHORITY
Cottus scorpius (type host)	Denmark	Müller	Müller 1788 : 6
Cottus scorpius	Gryphswald	Rudolphi	Rudolphi 1819 : 139
Cottus scorpius	Ireland	Bellingham	Bellingham 1844 : 254
Cottus scorpius	"Oresund e Berg," Sweden	Olsson	Olsson 1867 : 55
Cottus scorpius	Norway	Loennberg	Loenberg 1890 : 22
Cottus scorpius	Grafverna and Näset, Sea of Bahusia	Olsson	Olsson 1893 : 16
Cottus scorpius	Arctic Ocean	.....	Linstow 1901 : 281
Cottus scorpius	Gulf of Finland	Schneider	Schneider 1902 : 15

HOST	LOCALITY	COLLECTOR	AUTHORITY	
Cottus scorpius	Murman-Küste	Coll. Zool. Mus. K. Akad. Wiss., Petrograd	Linstow	1903 : 19
Cottus scorpius	White Sea	Danilevskij	Linstow	1903 : 49
Cottus scorpius	North Sea	Nicoll	Nicoll	1907 : 70
Cottus scorpius	Firth of Clyde, Millport, Scotland	Nicoll	Nicoll	1910 · 355
Cottus bubalis	England	Cobbold	Cobbold	1858 : 157
Cottus bubalis	Norway	Loennberg	Loennberg	1890 : 22
Cottus bubalis	Sweden	Loennberg	Loennberg	1891 : 51
Cottus bubalis	Grafverna and Näset	Olsson	Olsson	1893 : 16
Cottus bubalis	North Sea	Nicoll	Nicoll	1907 : 71
Cottus quadricornis	Gulf of Finland	Schneider	Schneider	1903 : 75
Pleuronectes boscius	Naples	Rudolphi	Rudolphi	1819 : 139
Pleuronectes flesus	"Oresund e Berg"	Olsson	Ariola	1900 : 396
Pleuronectes maximus	Denmark	Müller	Müller	1788 : 6
Pleuronectes maximus	Gryphswald	Rudolphi	Rudolphi	1819 : 139
Pleuronectes maximus	Ireland	Bellingham	Bellingham	1844 · 254
Pleuronectes maximus	Langrunne, Rennes	Dujardin	Dujardin	1845 : 618
Pleuronectes rhombus	Naples	Rudolphi	Rudolphi	1819 : 139
Pleuronectes rhombus	Ireland	Drummond	Bellingham	1844 : 254
Pleuronectes solea		Kais.-König. Nat'l Kab.	Leuckart	1819 : 40
Torpedo ocellata	Naples	Rudolphi	Rudolphi	1819 : 139
Torpedo oculata		Volz	Volz	1900 : 55
Gadus aeglifinus	Arctic Ocean		Linstow	1901 : 281
Gadus minutus	Naples	Rudolphi	Rudolphi	1819 : 139
Arnoglossus boscii	Naples	Rudolphi	Ariola	1900 : 396
Arnoglossus pegosa	Ariminus	Rudolphi	Rudolphi	1819 · 139
Arnoglossus solea		Mus. Vienna	Rudolphi	1819 : 139
Trigla adriatica	Hafnia	Eschricht	Diesing	1850 : 594
Trigla lineata	Ireland	Drummond	Diesing	1850 : 594
Psetta maxima	England	Siebold Coll., Brit. Mus.	Baird	1853 : 89
Platessa plana	Pennsylvania	Leidy	Leidy	1855 : 444
Platessa flesus	Germany		Lühe	1910 : 25
Platessa passer	Trieste		Stossich	1898 · 116
Rhombus maximus	Italy	Molin	Molin	1858 : 134
Rhombus maximus	Patavia	Molin	Molin	1861 : 235
Rhombus maximus	"Oresund e Berg"	Olsson	Olsson	1867 : 55
Rhombus maximus	Trieste	Stossich	Carus	1885 : 120
Rhombus maximus	Venice	Ninni	Stossich	1890 : 7
Rhombus maximus	Warnemünde		Matz	1892 : 105
Rhombus maximus	Rossitten, Cranz, Memel		Muehling	1898 : 36
Rhombus maximus	Trieste		Stossich	1898 : 116
Rhombus maximus	Genova	Parona and Ariola	Ariola	1900 : 395
Rhombus maximus	Trieste	Stossich	Stossich	1901 : 97

HOST	LOACLITY	COLLECTOR	AUTHORITY
Rhombus maximus	Gulf of Finland	Schneider	Schneider 1902 : 15
Rhombus maximus	North Sea	Nicoll	Nicoll 1907 · 72
Rhombus barbue		Volz	Volz 1900 : 55
Rhombus laevis	"Oresund e Berg"	Olsson	Olsson 1867 55
Rhombus laevis	Grafverna and Näset	Olsson	Olsson 1893 · 16
Rhombus maeoticus	Odessa	Nordmann	Linstow 1901 : 281
Lophopsetta maculata	Martha's Vineyard, Mass	Linton	Linton 1890 : 732
Bothus maculatus	Woods Hole	Linton	Linton 1898 : 430
Hemitripterus americana		U S Nat Mus.	Linton 1898 · 430
Hemitripterus americana	Casco Bay, Maine	U S Nat Mus.	Linton 1898 · 430 Linton 1898 · 430
Hemitripterus americana	Woods Hole	U S Nat. Mus.	
Limanda ferruginea	Block Id	U S Fish Com.	Linton 1898 : 430
Limanda ferruginea	Woods Hole	Linton	Linton 1901 : 485
Labrus maculatus	"Oresund e Berg"	Olsson	Ariola 1900 : 396
Motella mustela		Mus Vienna	Ariola 1900 : 396
Mullus barbatus	Genova	Parona	Ariola 1900 : 396
Solea monochii		Mus Vienra	Ariola 1900 : 396
Acipenser ruthenus		Volz	Volz 1900 : 55
Scorpaena porcus		Volz	Volz 1900 : 55
Paralichthys oblongus	Woods Hole	Linton	Linton 1901 : 484
Lota vulgaris	Dvina-Fluss	Danilevskij	Linstow 1903 : 19
Raja clavata	Black Sea	Pilat	Pilat 1906 : 191
Anguilla vulgaris	River Dee, Scotland	Scott	Scott 1909 : 79
Decapterus punctatus	Woods Hole Region		Sumner, Osburn and Cole 1913 : 586
Hippoglossus hippoglossus	Woods Hole Region		Sumner, Osburn and Cole 1913 : 586
Myoxocephalus aeneus	Woods Hole Region		Sumner, Osburn and Cole 1913 : 586
Myoxocephalus octodecimspinosus	Woods Hole Region		Sumner, Osburn and Cole 1913 : 586
Palinurichthys perciformis	Woods Hole Region		Sumner, Osburn and Cole 1913 : 586
Paralichthys dentatus	Woods Hole Region		Sumner, Osburn and Cole 1913 : 586
Pseudopleuronectes americanus	Woods Hole Region		Sumner, Osburn and Cole 1913 : 586

HOST	LOCALITY	COLLECTOR	AUTHORITY
Scomber scomber	Woods Hole Region	.....	Sumner, 1913 : 586 Osburn and Cole
Trachurops crumenophthalmus	Woods Region	.....	Sumner, 1913 : 586 Osburn and Cole
Uropkycis chuss	Woods Hole Region	.....	Sumner, 1913 : 586 Osburn and Cole
Hemitripterus americanus	Passamaquoddy Bay, New Brunswick	A. R. Cooper	Cooper (the present paper)
Hemitripterus americanus	Brandy Cove, St. Croix R., New Brunswick	A. R. Cooper	Cooper (the present paper)
Hemitripterus americanus	Woods Hole	V. N. Edwards	Cooper (the present paper)
? *Myoxocephalus aeneus*	Woods Hole	V. N. Edwards	Cooper (the present paper)
? *Myoxocephalus groelandicus*	Woods Hole	V. N. Edwards	Cooper (the present paper)

Most of the specimens studied ranged in length from 50 to 240mm., but none of them were considered to be complete posteriorly. The smallest measured 28mm. in length and the largest 677mm. The scolex assumes a variety of forms in preserved material, but agrees in general with the descriptions of that of *B. scorpii* given by all the authors from the time of Rudolphi (1810: 51). Its commonest shape is shown in figures 21 and 22 where it is seen to be quite elongated, somewhat broader and truncated anteriorly and narrow posteriorly. The anterior portion is in reality in the form of a low pyramid, comparable internally as well as externally with the terminal disc of the Triaenophorinae. Its base is deeply indented dorsoventrally, that is opposite the bothria, but rounded laterally. The whole scolex is broadest at about its middle and narrowest at its posterior end. A portion of the latter is here considered to be the beginnings of the first segment on account of its being constantly set off from the rest of the scolex ahead by a more or less definite groove. The bothrium is in the form of an elongated V, being ordinarily widest and deepest just behind the terminal disc and much narrower and shallower posteriorly where it is not bounded by a definite wall but spreads out on the base of the scolex. In many specimens, however, the scolex is so contracted and the walls of the bothrium so protruded that the latter shows its greatest depth at the middle of the scolex. In lateral view (Fig. 22) the scolex is more nearly oval in outline since it is a little wider towards the base. From this fact it is conceivable that Müller's (1788, Fig. 7) showing a more "orbicular" scolex in *B. scorpii* in lateral view may be explained by supposing that he was dealing with a much contracted specimen, altho in justice to the other side of the question, it must be said that the first segments in his figure are by no means contracted. It will be noticed that the figures of the scolex given here agree

very closely with that of Scott (1909, Fig. 3, Pl. V). However, from the fact that he records *B. scorpii* as having been found in *Anguilla vulgaris*, it is quite possible that he had in reality *B. claviceps* (Goeze) which has been found only in eels up to the present, so far as the writer is aware.

Segmentation begins immediately behind the scolex, so that there is no true neck. The base of the scolex, nevertheless, has the appearance of a very short neck region from which the foremost segments are cut off as soon as they form. Such in fact is considered to be the case. The anterior part of the strobila on the other hand serves the purpose of a neck in that it shows a division into subsegments in a manner to be presently described. As regards the habit of the whole strobila and the general shape of the segments, Rudolphi's (1810:51) description of the species is so applicable to this form that it is given verbatim:

"*Collum* nullum. Corpus planum, margine crenato. *Articuli* capiti proximi plerumque longissimi, angustissimi, subcuneati, margine postico untrinque parum exstante, saepe tamen, praesertim post mortem, contracti, ut reliquis vix longiores appareant. Articuli insequentes anticis breviores et sensim latiores; postici subaequales, fere quadrati, ut plurimum latiores quam longi, interdum quasi ex duobus tribusve confusis compositi, satis magni, margine obtusiusculo hinc inde inciso. Articulus ultimus obtusus.

Linea utrinque longitudinalis articulos majores percurrit. Inter utramque faeturae apparatus."

Leidy (1855:444) described the strobila of the *B. scorpii* which he found in *Platesa plana* as follows: "Neck none. Anterior segments cuneate or triangular; posterior ones quadrate; each with an appearance of three subdivisions, with the subsegments having a pair of generative apertures, in the course of a longitudinally depressed dark colored line, passing the length of the body." Cobbold (1858:157) said of individuals from *Cottus bubalis*: "Toward the lower part of the so-called neck, the joints exhibited at the lateral margins indications of division, which became gradually more defined towards the tail." In the same connection Krabbe (1865:37) stated that, according to Eschricht, "Pendant leur développement ultérieur, l'augmentation du nombre des articles n'est pas toujours exclusivement due, comme chez les Taenias, à la formation de nouveaux articles engendrés par la tête, mais chez quelques espèces, telles que les *B. dubius, variabilis* et *fasciatus*, [here *B. punctatus* also] elle est encore produite par la division transversale qui s'opère dans les articles déjà formés." Olsson (1867:55) also referred to multiplication of segments by transverse division of older ones. Loennberg (1891:52) denied this statement of Olsson's, but, as pointed out below, the negation is applicable to the posterior mature segments of this form at least, not to the middle segments referred to by the latter. Linton (1890:773) said "Secondary segments appear at about the twelfth segment from the head. These are formed by a division of each segment into two by means of a median transverse line. This is repeated farther back in much the same manner as described under *D. microcephalum*." In this form such subdivision of segments to form daughter segments occurs

all along the strobila from close behind the scolex to well into the region showing the median row of reproductive rudiments, and in such a manner that, in the anterior part of the strobila at least, what is considered to be a primary segment, situated between the most prominent transverse furrows, becomes subdivided into 2, 4, 8, 16 and finally 32 divisions, each of the latter accommodating two reproductive rudiments. But it must be emphasized that this method of formation of new segments is not strictly followed out, since as it passes backward in development, the primary segment does not always contain 64 genital rudiments. In the first place, some secondary or even tertiary transverse furrows become almost as prominent as the primary ones, and secondly, there is at the same time considerable further subdivision not only of the peripheral tissues but especially of the rudiments themselves. Close behind the scolex the primary segments are very short (Fig. 55), the first six to ten being divided only into two subdivisions in strobilae of moderate size, but into three or four subdivisions in the largest chains. Farther back this process of segmentation takes place gradually; but division is usually seen to occur more readily and quickly in the anterior part of the primary segment or of its major subdivisions, i.e., secondary or tertiary, than in its posterior part—occasionally however the reverse being the case. Thus in general there is a sort of dominance of the anterior end of the segment, which one might call a zooid in the sense in which Child uses the word, over its posterior end as regards metamerism. While this method of formation of segments is further obscured by the fact that often one sees intercalated among primary segments, showing these features well, others which seem to lag behind in division and are hence younger, and that in much elongated strobilas it is still more difficult to distinguish between primary and secondary transverse furrows, owing to their being quite smoothed out especially medially, the whole plan is sufficiently clear to warrant its being described with the definiteness here given. Figures 56 and 57 will give a better idea perhaps of the whole method of segmentation than this description. While in figure 55 the primary segments are indicated by asterisks, in figures 56 and 57 the whole drawing is in each case that of a primary segment. Under the heading of the reproductive system below it will be seen that in the mature portion of the strobila the most prominent transverse furrows are described as coming approximately every eighth or sixteenth genital segment. This is due to the fact that the secondary and tertiary furrows, respectively those dividing the primary segments into two then four parts, become quite as pronounced as the primary ones, thus making it very difficult to follow this plan of segmentation beyond the region of differentiation of the genital rudiments.

At least three prominent longitudinal grooves run thruout the median and posterior portions of the strobila on each surface, even cutting thru the posterior borders in many places. Their course is not regular and they are accompanied by numerous other shorter and more irregular grooves, some of which, but not all, are due simply to lateral contraction of the segments.

The following table gives a list of measurements of representative specimens in alcohol:

Total length in mm.	234	173	130	51	677	*233	*180
Length of scolex	1.20	1.07	0.81	1.14	1.11	5.00	0.85
Breadth of terminal disc	0.30	0.33	0.26	0.33	0.28	0.29	0.27
Breadth at middle	0.35	0.32	0.30	0.37	0.31	0.11	0.22
Breadth at base	0.28	0.27	0.24	0.35	0.26	0.11	0.16
Length of first segment	0.14	0.16	0.09	0.18	0.33	1.83	0.44
Length of posterior segment	0.85	0.46	0.35?	0.57	?	0.54?	0.81
Breadth of same	1.83	1.12	0.53?	0.92	?	1.70	0.99
Maximum breadth of strobila	2.50	1.60	1.05	1.57	3.35	2.80	1.51

*Somewhat stretched during fixation.

Since Lönnberg (1891:52) described the cuticula of the species there has been no mention of it in the literature, so far as the writer is aware. It was found to be 5μ in thickness and composed of two layers, the outer of which is about two-fifths of the whole thickness and is made up of rather stout, closely set "cirri" which stain much more readily than does the inner more homogeneous and lighter layer. These cirri seem to lie on a distinct membrane since their proximal (central) ends are all even and distinguishable in some places as dark granules. In sections stained more deeply than those which show the inner layer as a single homogeneous stratum, the latter is divided into two layers, the outer of which is less deeply stained than the inner and about one-half as thick or one-fifth of the thickness of the whole cuticula. The wavy nature of the cuticula and the basement membrane is as described by Lönnberg, but in many places the membrane is separated from the cuticular musculature by a very thin clear space barely distinguishable with high powers. The cuticula covering the scolex is about 4μ thick, the difference between it and that over the proglottides being due to a thinner homogeneous stratum. The outer layer of the cuticula is not modified to form spinelets on the posterior borders of the proglottides, nor on the edges of the terminal disc, as in *C. crassiceps*, but the pseudocilia are somewhat longer and relatively stouter on the scolex and anterior segments than elsewhere.

The subcuticula, from 25 to 30μ in thickness, has the nuclei of its spindle-shaped cells arranged at various levels so that the space between the cuticula and the vitelline follicles is, excepting for its outer one-third, well filled with them (Fig. 84).

The chalk-bodies, described by Lönnberg, were not studied in living material; but spherical spaces which were evidently occupied by them before they were dissolved out by the acetic acid of the fixing agent, were found to be more

numerous, as Lönnberg stated, in the cortical than in the medullary parenchyma. In the scolex, however, they are somewhat more numerous than in the strobila, in both of which locations they attain a diameter of 13μ.

Lönnberg (1891:53) gave a good description of the musculature of the species, while Lühe (1897a:747) referred to that of the posterior border of the proglottis in the discussion of the arrangement of the muscles of the whole order. In addition to corroborating the findings of these authors, it was noticed by the writer that the fibres of the transverse series are mostly confined to the very short regions between the sets of reproductive organs and are most numerous just ahead of the prominent segmental furrows mentioned above, this applying to both the inner and outer lots. Towards the median line each layer of longitudinal muscles is about 35μ in thickness and composed of bundles of various sizes, in which the fibres are very closely arranged. The outer longitudinal muscles, the extension of which into the posterior borders of the segments immediately behind the scolex are only weakly developed, are in the scolex confined almost completely to very thin bands situated close to the cuticular musculature in the edges of the bothria, as described elsewhere by the writer (1914a:92) for *H. globuliforme*.

Lönnberg (1891:54) described the nervous system so well that little needs to be added. The foremost four large branches from the brain complex were not found to be relatively as large as those shown in Lönnberg's Figure 1a, and the commissure appeared to be divided into two, not distinctly separated, frontal strands, the whole depth of which, including the space between them, was not as much as that shown in his Figure 1c. In the strobila the chief nerve strands, each from 15 to 25μ in diameter, are situated towards the ventral side of the medulla and at the junctions of the lateral and median quarters of the latter, as shown in figure 84.

The excretory system of *B. scorpii* was described in detail by Fraipont (1881:8), while Lönnberg (1891:53) added some further notes on its structure, the former, however, working on living material in which the canals are much more readily seen. In good toto preparations the "canaux descendants" may be easily seen in segments showing the reproductive rudiments as well as farther forward. Owing to a mere accident, temporary preparations showing the details of the reticulum of descending canals in great detail were made by the writer with more or less constant success. When some pieces of a strobila were being transferred from synthetic oil of wintergreen to a slide for the preparation of toto mounts by the further addition of xylol-damar, they suddenly became opaque white and remained so for some time after the damar and coverglass had been added. This opacity was found to be due to air having been drawn into the excretory canals not only thru their cut ends but thru the foramina secundaria. But since the superficial reticulum and all the finer canals were filled with air, nothing of the arrangement of the larger canals could be made out until a short time had elapsed, or until the preparation had been heated slightly. Then the air in the smaller canals became replaced by the xylol-damar, and the larger canals stood out as very distinct silver

threads. This sort of preparation is unfortunately not permanent, since after a few minutes all of the canals disappear, excepting the very largest which can still be followed as in ordinary toto mounts. The results of this method of demonstrating the excretory canals are shown in figure 61, a camera lucida drawing made while the canals were disappearing from view. Three of Fraipont's large "canaux descendants" can be seen together with much of the anastomes among them and at least two branches to foramina secundaria. The largest and most median canal has a diameter of 50μ. But contrary to what was stated by Fraipont (1881:9,11), only six of these main channels were found close to the ventral layer of longitudinal muscles in the medullary parenchyma, and not six for each surface of the strobila. Lönnberg stated, and correctly too, that their number is very variable as is their size and course, the whole forming a complicated reticulum showing the typical "island formation." As regards the termination of the excretory vessels at the posterior end of the strobila, the writer confirms Fraipont's (1881:10) statement that: "Chez un sujet qui a déjà perdu des proglottis, les gros canaux longitudinaux sont rompus au niveau du bord libre posterieur du dernier segment. Les uns communiquent directement avec l'extérieur, les autres ne sont renfermés et se terminent en cul-de-sac." But no cases were met with in the material at hand in which it could be considered that no segments had been lost. Towards the scolex the six vessels gradually come closer and closer together until in the first segments they may appear for short distances in two sets of three each, dorsoventrally situated; but farther on become lost in their anastomoses. Entering the scolex there may be seen four, three, or two main canals, but they cannot be followed as such thru many sections, since they soon break up into the reticulum mentioned by Fraipont as ramifying thruout the scolex.

Of the generative organs the earliest writers were able to discern only the external openings ("oscula") and the uteri which, showing their contained, dark brown eggs thru the body wall as a longitudinal series of dark punctations, gave origin to the specific names of Zeder (1800) and Rudolphi (1802 and 1810). Concerning these characters Müller (1788:6) wrote as follows:

"Margines corporis depressi intersectione articulorum crenati apparent; oscula in anterioribus articulis nulla adsunt, in posterioribus vera altera in pagina *pori* in macula albida nigricantes, in altera *papilla* alba subelevata, punctaque seu globuli utrinque dispalati, qui *ovula*. *Oscula* seu pori non seriem rectam in corpore. Taeniae sed hinc et illinc divergentem constituunt, alterum in centro articuli, alterum in intersectione constituum. Articuli postici reliquis latiores punctis utrinque dispersis medio autem coacervatis papillullamque exhibentibus repleti sunt; horum coacervatio oculo nudo punctum centri nigrum offert, armatus vero ovula seu globulos e membrana ovata pellucida punctulis nigricantibus impleta constantes discernit."

Rudolphi (1810:50) described them in these words:

"Singuli enim articuli in superficie dorsali nodulum orbicularem, simplicem vel duplicem, subelevatum, vel albidum vel fuscescentem aut nigrescentem

exhibent; in superficie autem ventrali nodulus simplex vel duplex, pariter, sed minus, exstans, quasi perforatus videtur; corporeque pellucido nodulis illis linea corporis media, plerumque tamen irregularis oritur. Noduli aperti *ovaria* sistunt, *ovisque* ellipticis mediocribus referti sunt, haec etiam saepe circa eosdem effusa sunt." From these descriptions it is to be seen that while Müller made correct observations concerning the relations between the positions of the genital openings and the transverse furrows mentioned above, Rudolphi considered the ventral surface to be that on which the openings of the cirrus and vagina are situated and the dorsal that on which the uterus opens to the exterior.

Van Beneden (1850) seems to have been the first writer to describe the anatomy, with however some errors of interpretation as pointed out by Lönnberg (1891). After Lönnberg's the best and practically the only description of the genitalia was given by Matz (1892:105), Ariola (1900:394) and Lühe (1910:25) obviously copying in part at least from him.

The earliest traces of the reproductive rudiments appear in toto mounts about 35 to 40mm. from the tip of the scolex. From this region backwards they increase in size, but so slowly that in large strobilas there may be an intervening stretch of at least 225mm. before the genital sinus appears. Then the rudiments differentiate very quickly, the first eggs appearing in the uterus-sac about 2mm. farther on in one toto mount made. In the largest strobila at hand the first genital sinuses were seen, when the worm was examined in alcohol, about 375mm. from the tip of the scolex, and the first traces of eggs showed thru the ventral body wall about 20mm. farther on.

Van Beneden (1850:162) was the first to mention the relations between the external segments and the sets of reproductive organs. He said: "Dans chaque anneau, il y a deux ou trois appareils mâles et femelles complets; je pense que ces anneaux se divisent encore plus tard, de manière à n'avoir plus qu' un appareil dans chaque animal," [here "animal" is evidently a misprint for "anneau"]; and further in his footnote referring to the superscript after "complets": "J'ai vu des anneaux qui en contenaient jusqu'à six." In his figure 4, Pl. XXI, he showed four parts of the strobila containing evidently three or four sets of reproductive organs in each segment, with the latter subdividing so that two sets appeared in each subsegment in the fourth part of the figure. Leidy described the posterior segments of *B. scorpii* as " . . . quadrate; each with an appearance of three subdivisions, with the subsegments having a pair of generative apertures, in the course of a longitudinally depressed, dark colored line, passing the length of the body." Linton (1890:733) referred to "the phenomenon which the posterior segments present of being welded together in groups of three or four, an appearance which is quite characteristic of the posterior segments and which has been alluded to in various descriptions of the species," while further, in connection with the apertures of the reproductive organs: "In the middle of the strobila there sometimes appear to be as many as four or more papillae to a single segment;" and with reference to the specimens from *Lophopsetta maculata*: " . . . toward the

posterior end of the body the adult segments are arranged in groups of from four to six simple segments, as if the latter were partially fused together, which is another characteristic of this species." From these statements and the further fact that the posterior proglottides have been described as trapezoidal (Stossich), quadrate (Rudolphi, Linton), subquadrate (Diesing), or at most, broader than long (Rudolphi)—actually about twice as broad as long from Linton's (1890:732, 734) description—it is evident that the groups of four sets of reproductive organs (much less frequently three, five or six) shown here in figures 59 and 60, and separated from each other by grooves which in alcoholic material appear to be complete, have been considered to constitute the ripe proglottides. But, as pointed out by Lönnberg, the lesser transverse furrows are only "greater wrinkles or foldings of the surface" and do not cut in deep enough to cause the parts immediately ahead to stand out distinctly like the posterior borders of the proglottides of other species, e.g., *C. crassiceps*. Such posterior borders, with their accompanying "complete" transverse furrows, do occur, however, but only at considerable intervals. One case is shown in figure 95, where it will be noticed there is no such distinct separation of the proglottis from the next one ahead. So far as the writer is aware, this has been pointed out only by Lühe (1910:25) who said: " . . . in reifen Gliederstrecken liegen zwischen zwei völlig durchgehenden, aber auch nur wenig hervortretenden oberflächlichen Querfurchen in der Regel 16 sehr kurze Genitalsegmente, die äusserlich voneinander nur durch Zackenbildungen des Seitenrandes gescheiden sind." In this connection it should also be noted that in his description of *Fimbriaria fasciolaris* (Pallas), a taenioid from various water birds, Wolffhügel (1900:94) remarked that it is comparable to *B. scorpii* in that "eine bis ins aussergewöhnliche gestiegerte Anzahl von Geschlechtsapparaten in einer Proglottis sich folge."

In a considerable length of one toto mount of this form there were found ahead of and including the region of differentiation of the reproductive rudiments the following consecutive number (from behind forwards) of genital segments between the most pronounced transverse furrows, that is in the primary segments in question: 67, 82, 101, 107, 90, 111, 116, using as the criterion of a genital segment, especially ahead of the region of differentiation, the aggregation of nuclei in the median line which will go to form the central organs and ducts of the sytem. There is, however, much difficulty in making these counts on account of rudimentary or intercalated groups of nuclei which, judging from conditions to be seen in the region of differentiation, may or may not form complete sets of genitalia, and above all of the further subdivision of many of these rudiments, which otherwise proceeds in quite the same manner (Fig. 57) as that of the external segments in the anterior part of the strobila. Furthermore, there may often be seen either in the anterior part of the region of differentiation or much farther ahead (Fig. 57) a lateral doubling of the developing genitalia. But since no case was met with of two sets of reproductive organs in a ripe genital segment, it was concluded, especially because of the great infrequency of this duplication, that one or the other rudi-

ment eventually gets the upper hand and develops at the expense of the other. This is borne out by the fact that in half the cases one rudiment was much larger than the other. The above mentioned groups of rudiments were divided and subdivided by less and less pronounced transverse furrows in the following manner:

67				82					101						
43		24		35			47		54				47		
24	19	10	14	14	21	18	13	16	16	14	12	12	20	12	15

This continued until eventually the groups of four (or five, rarely six) sets of genitalia of the authors could be made out. Each of these in turn was seen to be divided into two groups of two sets each, so that each lateral crenulation corresponded to two (or three) of them, i.e., to the 1-32nd division described above (Fig. 57). In ripe segments this arrangement may obtain or the segment may divide again peripherally, so that each crenulation then corresponds with one set of genitalia (Figs. 59 and 60). The latter figures show that "complete" transverse furrows are present between every 8 or 9 (sometimes 7, or apparently even 3, 4, 5 or 6!) genital segments. However, other more relaxed strobilas in alcohol showed complete furrows only every 16 to 17 sets of genital segments, there often being a group of 5 instead of the much more common group of four—but in the same neighborhood of the strobila just as complete grooves every 8, 9 or 10 sets. This shows that a grouping of the genital segments into lots of approximately 16, as mentioned by Lühe (1910:25) is so irregular that it can scarcely be said to occur "as a rule," and that the peculiar method of segmentation of the anterior end of the strobila mentioned above (p. 102) is very difficult to follow with any degree of certainty beyond the region of differentiation of the genital rudiments.

The genital sinus is situated on a low papilla (Fig. 59) on the dorsal surface, in the median line and from one-half to two-thirds of the length of the genital segment from its anterior border, while the uterine opening on the ventral surface is located much farther forward, even at the bottom of the groove corresponding to the indentation of the edge of the strobila, separating the crenulations mentioned above. The sinus itself is circular in outline and from 40 to 45μ in diameter by 15 to 20μ in depth. At its bottom the cirrus and vagina open close together, the latter immediately behind the former, thru a secondary sinus or ductus hermaphroditicus, the walls of which are often found protruding thru the opening of the larger vestibule as if to form part of a functional cirrus (Fig. 95).

The testes are arranged in two lateral fields in the medullary parenchyma, as pointed out by Lönnberg, and are continuous from segment to segment, altho they show some tendency towards division interproglottidally. The number was given by Matz (1892:106) as about 76, with their size as 40.8μ, but here it was found to be from 30 to 60, while their size was 35 to 70μ, 60 being the

commonest measurement. The vas deferens, filled with sperms, forms a compact mass of coils about 0.18 by 0.10mm. in size, lying irregularly to the right or left of the uterine duct or slightly behind the sac and immediately alongside the cirrus-sac, as shown in Fig. 71. The ductus ejaculatorius portion of the vas deferens within the cirrus-sac, that is, that part occupying the lowermost one-third of the latter, has a diameter of from 4 to 6μ. The middle stretch of the duct often expands to 13μ, while the distal part, the cirrus proper, has a maximum length of 65μ with a width of 14μ. Matz gave the dimensions of the organ (? the cirrus-sac) as 100 by 50μ. The cuticula lining the cirrus is pseudoiliated on its inner (functionally outer) surface, somewhat as is that on the external surface of the worm. The cirrus-sac is located at right angles to the dorsal surface (Fig. 95) and extends only a short distance into the medulla, as compared to other species. It is ovoid in shape, with the narrower end towards the cloaca, and from 115 to 120μ in length by from 75 to 80μ in diameter. Its wall is composed of an inner thick layer of circular muscles and a very thin outer layer, the fibres of which are directed somewhat obliquely, the whole being 8μ in thickness. As pointed out by Lönnberg and shown in figure 95, the organ is peculiar in that its wall is coated both externally and internally with a thick layer of nuclei which are doubtless mostly myoblastic in their nature. An aggregation of nuclei at the lower pole of the sac, surrounding the vas deferens and continuous with the layer of nuclei on the outside of the pouch, are too numerous to be considered as myoblastic nuclei only. They do not seem to be mentioned either by Lönnberg or Matz. Their arrangement would indicate that they are possibly prostatic in their nature, the whole structure having the appearance of a gland. Retractor muscles of the cirrus proper are scarce. This fact, taken in conjunction with the further fact that the wall of the sac is quite thick and powerful, and that Lönnberg saw only a short thick cirrus when protruded, would lend support to the view that the latter is quite small and not very important from a functional standpoint. Concerning copulation in this species Lönnberg said: "Es ist daher wahrscheinlich, dass die normale Befruchtung so vor sich geht, dass das Sperma in den Sinus genitalis hinausgepresst wird, und davon entweder passiv durch die Kontraktion der Sinus genitalis oder aktiv durch eigene Bewegung in die Vagina gelangt. Sowohl die eine als die andere Weise scheint recht möglich zu sein, weil die Mündung der Vagina ganz neben derjenigen des Penis gelegen ist."

The vagina opens into the ductus hermaphroditicus close behind the cirrus. From there it proceeds close along the cirrus-sac to its lower end, and then turns back to pass over the ovarian isthmus and into the generative space. Its diameter is 13μ, while its wall is composed of a cuticula 5μ in thickness and a thin layer of circular muscles. Its cuticula is retained until the point of union with the oviduct is reached, where the lumen narrows down suddenly to one-half the former diameter (Fig. 105). The ovary with a width of 0.35mm. and a length of 0.15mm., is somewhat irregularly "biscuit-shaped" (Fig. 71) and situated close to the posterior border of the segment or protruding slightly into the segment behind. It is composed of short tubular lobules of varying

size. In transections it is seen to be "concave towards the surface bearing the genital openings" owing to the fact that the ventrally situated isthmus is quite narrow and thick and consequently not well separated from the lobular wings which extend thruout the whole dorsoventral diameter of the medulla and also somewhat enfold the former posteriorly in the median line. Ova from the isthmus are 15μ in diameter, while their nuclei and nucleoli average, respectively, 7 and 3μ. The oocapt is quite muscular, and 35μ in diameter. The oviduct proceeds dorsally for a short distance only before it is joined by the vagina at a vestibule into which the oviduct itself opens (Fig. 105) by a narrow slit much as in *C. crassiceps*. The wall of the duct is composed of an epithelium, in which no cell-boundaries could be made out, but provided with cilia directed towards the uterus. The oviduct continues dorsally for a short distance with the same structure and diameter, namely 18μ, to take on the vitelline duct dorsal to the anterior edge of the isthmus. The vitelline follicles are arranged in the cortical parenchyma in two lateral fields (Fig. 84) which are, however, slightly connected with each other dorsally and ventrally in the median line by a few isolated follicles. No large follicle such as that described by Matz in the neighborhood of the ovary was seen in the material studied. The follicles vary somewhat in size, but average 35 to 55μ in diameter, are very closely crowded together—so as to obscure in toto preparations the testes beneath them—and continuous from proglottis to proglottis. The latter fact makes it difficult, if not somewhat unnecessary, to state the number for each genital segment, but using Matz's method of multiplying the average number seen in transections by that seen in sagittal sections (here the average of several segments was taken), the number varies from 350 to 540, or 440 on the average. Matz gave 490 as the number. Two main vitelline ducts proceed from opposite sides of the genital segment and unite in the antero-dorsal portion of the generative space to form a very short common duct which from the amount of yolk it usually contains may act as a vitelline reservoir, altho the same function is shared even to a larger degree by the much coiled and distended proximal portions of the separate ducts. A few cases were met with in which small ducts laden with yolk came from follicles clearly belonging to the genital segment following. This condition is, however, not surprising in view of the continuous arrangement of the follicles themselves. The diameter of the common duct at its point of union with the oviduct is about 8μ. The very voluminous shell-gland is situated dorsal to the ovarian isthmus close behind the cirrus-sac, with a depth of 85μ and width of 115μ. The uterine duct is quite capacious since it is composed of many coils extending thruout the whole depth of the medulla immediately ahead of the ovary. Proximally it is lined with a syncitial epithelium which distally becomes much attenuated. While it is usually situated in the median line it may alternate from right to left as a whole according as the vas deferens does so on the opposite side of the proglottis, the uterus-sac in such cases remaining in the median line. As above noted, the uterus-sacs were called "ovaries" by the early writers. They were seen thru the body wall to be filled with the characteristic dark brown eggs forming dark patches or

punctations, hence the specific names *bipunctata* and *punctata*. In this species the uterus-sacs were described by Rudolphi, Leuckart (1819:41), *et al.*, as arranged in a single row, in a double row, or alternating thruout the strobila. They were likewise found to alternate irregularly from side to side (Fig. 60) (e.g., r, l, l, r, r, l, r, l, l, r, r, l, etc.) or to be more medially situated (l, m, l, m, m, m, m, l, m, r, r, m, l, l, m, m, etc.) but never in two rows, excepting in a very few immature genital segments (Fig. 57), unless the alternating condition in much contracted strobilas is considered as such. While the sac has a diameter of about 0.18mm. when the first eggs appear in its lumen, it may reach a length of 0.35mm. and a transverse diameter of 0.22mm. or about one-sixth of that of the proglottis. The combined uterus-sac and uterine duct may in many cases occupy more than one-third of the width of the segment. The hindermost segments, in which the uterus-sacs may be gorged with eggs to a diameter of 0.65mm., separate from the chain evidently in pairs, the lines of division taking place at the furrows between the larger crenulations mentioned above. No detached proglottides were found free, however, in the intestine of the host, altho Olsson (1867:55) recorded having found such, while Weinland (1858:9) said that, according to Eschricht, the species "which lives in the sculpin of the Baltic (*Cottus scorpius*) throws off its whole chain of joints every year and then sends out a new one from the neck." Like that of the distal portion of the uterine duct the wall of the sac is composed of a much attenuated epithelium from the basement membrane of which the nuclei, separated by wide intervals, project into the lumen like bosses. The uterus-opening is situated ventrally in the middle of the uterus-sac, and with regard to the external segmentation either in the middle of the larger (double) segment or in the groove separating it from the next ahead or behind. Circular in outline and 50μ in diameter, it is surrounded by an area of radiating nuclei, thought by Lönnberg to be possibly of the nature of a gland for the secretion of a material of use in the passage of the eggs to the exterior. The actual opening is formed by the rupture of a membrane guarding the outlet, which has a thickness of from 15 to 30μ, (cf. *C. crassiceps*).

The fresh egg is ellipsoidal in shape, dark brown in color, and measures from 66 to 80μ in length by 43 to 45μ in transverse diameter. The shell was observed to be about 9μ thick in living material and not provided with an operculum. No mature eggs showing the six hooks of the oncosphere were met with in fresh material in the field.

Nothing was discovered regarding the intermediate host or hosts of this species, not even in the way of food-contents, for the stomachs and intestines of the few sea-ravens examined were all found to be empty. Linton (1890:732) gave as the food of *Lophopsetta maculata* and *Limanda ferruginea*, from which he recorded *Dibothrium punctatum* Rud., "several species of Annelids, fragments of Squilla, and several specimens of a species of Margarita." No specimens smaller than about 25mm. in length were obtained. According to Udinsky's abstract, Pilat (1906:191), working on *B. scorpii* from *Raja clavata* of the Black Sea (the only case of the species having been found in a selachian

fish, so far as the writer is aware) established the fact "dass seine Larven in den verschiedenen Fischen oder Tieren, welche von Rochen (*Raja clavata*) gefressen werden, sich befanden."

From the foregoing description it is to be seen that this form is very closely related to the *B. scorpii* (Müller) of Europe, altho in many respects it is so different as to almost warrant the erection of a new species to accommodate it. However, on account of the fact that several forms of the European species have been reported, namely, *B. scorpii forma bubalidis* and *forma motellae* by Lönnberg (1889:32 and 1893:13) and those from *Rhombus maximus* and *Cottus quadricornis* by Schneider (1902a:14 and 1903:75), it is considered that here in America one finds the same species as has been found in Europe. And from a comparison of the measurements given above with those given by Leidy (1855: 444) and Linton (1890:732, 734 and 1897:430), it seems that, little as one can rely on external measurements, they also point to definite differences of habit as this worm is found in different host species on this side of the Atlantic.

In the table given below under *B. claviceps* the important diagnostic data of this form are placed alongside those of the European species for the sake of comparison.

The material studied consisted of lots Nos. 191, 196, 197, 198, 287, and 288 of the writer's collection from the intestine of *Hemitripterus americanus* (Gmelin), No. 17.57 of the Collection of the University of Illinois from the same host, and No. 17.56 of the same collection from *Myoxocephalus aeneus* (?).

DIBOTHRIUM ANGUSTATUM (Rudolphi), species inquirenda

Linton (1901a:454, 474) reported this species from *Poronotus triacanthus*, the butter-fish, and *Merluccius bilinearis*, the silver hake. Regarding specimens from the former he said: "9. *Dibothrium angustatum* Rudolphi. Intestine [Pl. XXIV, figs., 269, a, b, c.]

Thirty-seven young strobiles, August 21, 1899. These agree closely with Diesing's synopsis of this species: 'Head elongate, tetragonal, slender, with oblong lateral bothria; neck very short. First segments elongated, very narrow, succeeding segments shorter, subquadrate.'

The outline of the head varies with the state of contraction, but the prevailing form is linear, oblong or somewhat clavate. Segments slender, almost cylindrical, slightly enlarged at their posterior ends. Dimensions of an alcoholic specimen in millimeters: Length of head, 1.16; breadth, anterior 0.33, greatest breadth 0.33, posterior 0.19. Another: Length of head 1.21, breadth anterior 0.22, greatest breadth 0.26, posterior 0.17. Longest head measured 1.92mm. in length to the first distinct segment. The strobiles are linear or nearly so and measured about 25mm. in length."

The species was originally created by Rudolphi (1819:476) to accommodate two specimens from *Scorpaena scrofa*. The diagnosis he gave, however, applies not only to the anterior end of *B. scorpii* when much elongated, but also to younger specimens of the same. "Ovaria speciei praecedentis [*B. punctatus*—mihi] cui haec etiam valde affinis est," from the same description

strengthens this fact, as does Diesing's (1850:594) remark that *D. angustatum* "speciei praecedentis forsan mera varietas." Dujardin (1845:614) considered the species to be synonymous with Leuckart's (1819:41) *B. affinis* which the latter pointed out was "ähnlich dem *B. punctatus*," only smaller and more elongated. An interesting point that Leuckart brought out, which further strengthens the resemblances to *B. scorpii*, was that "Ein grösseres Glied wechselt gewöhnlich mit einem kleineren ab." "Ovaries" were described as being in one row and nearer the anterior than the posterior edge of the proglottis, which with the general characters of the segments and scolex point to *B. affinis* being merely a variety of *B. scorpii*. Later Diesing (1863:240) added to the diagnosis: "Aperturae genitalium laterales"—that is surficial, and not lateral in the sense of being marginal, as it is now used. Parona (1887:320) gave a description of the external features which differed little from those already published and even with the four figures accompanying it does not permit one to separate the species from *B. scorpii*. Matz (1892:121) merely listed the species, while Blanchard (1894:701) included it in his genus Bothriocephalus. Ariola (1896:263, 272, 280) made a few brief statements regarding the form, in which, besides giving the length and breadth of the strobila as 8.5 to 9cm. and 0.9mm. respectively and the dimensions of the eggs as 70 by 51μ, he said that "Osservo che esso tanto per le dimensioni del corpo, quanto per i caratteri dello scolice nulla ha di comune col *B. punctatus*, che ha una lunghezza totale di circa 50cm., e quindi constituisce una specie propria, quale appunto l'hanno ritenuta il Rudolphi, il Parona, ed altri elmintologi." He placed the species (p. 280) among those of the genus Bothriocephalus Rud. with dorsoventral bothria, in his classification of the family "Bothriocephalidae s. str." Stossich (1898:116) reported the species from *Scorpaena porcus* at Trieste, but added nothing of diagnostic value, while Ariola (1900:419) continued to hold his former opinions concerning the form: "E con ciò cade il dubbio di Diesing e di Carus, che cioè il *B. angustatus* possa riguardarsi come una varietà del Botriocephalo puntato, il quale ultimo ne è assai lontano, oltre che per notevoli differenze di tutto il corpo, per i botridii dorsoventrali." Linton's report of the species has been referred to; and finally Shipley recognized the species in "Numerous fragments taken from the intestine of the salmon, *Salmo salar*."

Thus it is evident that in the literature there are not sufficient data to enable one to state whether this form is a separate species or not, but much that points to its being only a variety of the quite variable *B. scorpii*. Nor was the writer lead to any conclusions by an examination of the material which Linton (1901:474) described from *Merluccius bilinearis*, contained in No. 6646, U. S. N. M. It was found to be very fragmentary and immature, but on the whole to suggest *B. scorpii* in miniature. A toto preparation of one of the widest pieces showed no traces of the reproductive rudiments, but six chief excretory vessels, arranged quite like those in *B. scorpii*, the median pair being the largest, and all of them quite straight as from pronounced elongation of the whole stretch of segments. On the other hand, the long narrow condition of the scolex seemed to be persistent in the material; but, since no strobilas of *B.*

scorpii nearly so small were at hand for study, the writer cannot say that such characters do not exist in the latter. On the whole it seems best to consider *B. angustatus* a *species inquirenda* until more and better material can be studied and comparisons made between the form that appears here in America and that which is found in Europe.

BOTHRIOCEPHALUS CLAVICEPS (Goeze 1782)

[Figs. 19, 20, 23, 72, 85, 96]

1722	*Vermis multimembris*	Leeuwenhoek	1722 : 490
1780	*Taenia anguillae* (part.)	Müller	1780 : 208
1782	*Taenia claviceps*	Goeze	1782 : 414
1786	*Taenia claviceps*	Batsch	1786 : 211
1786	*Taenia anguillae*	Batsch	1786 : 233
1790	*Taenia anguillae*	Gmelin	1790 : 3078
1790	*Taenia claviceps*	Schrank	1790 : 46
1800	*Rhytelminthus anguillae*	Zeder	1800 : 215
1801	*Taenia claviceps*	Rudolphi	1801 : 103
1802	*Taenia anguillae*	Bosc	1802 : 307
1803	*Rhytis claviceps*	Zeder	1803 : 293
1810	*Bothriocephalus claviceps*	Rudolphi	1810 : 37
1816	*Bothrioc. claviceps*	Lamarck	1816 : 582
1819	*Bothrioc. claviceps*	Rudolphi	1819 : 136, 472
1819	*Bothrioc. claviceps*	Leuckart	1819 : 49
1824	*Bothrioc. claviceps*	Nitzsch	1824 : 97
1844	*Bothrioc. claviceps*	Belilngham	1844 : 251
1845	*Bothrioc claviceps*	Dujardin	1845 : 618
1848	*Bothrioc. claviceps*	Siebold	1848 : 147
1850	*Dibothrium claviceps*	Diesing	1850 : 589
1853	*Bothrioc. claviceps*	Baird	1853 : 89
1854	*Dibothrium claviceps*	Diesing	1854 : 578
1859	*Dibothrium claviceps*	Polonio	1859 : 225
1859	*Dibothrium claviceps*	Molin	1859 : 8
1863	*Dibothrium claviceps*	Diesing	1863 : 241
1867	*Bothrioc. claviceps*	Olsson	1867 : 56
1885	*Bothrioc. claviceps*	Carus	1885 : 120
1892	*Bothrioc. claviceps*	Matz	1892 : 108
1893	*Bothrioc. claviceps*	Olsson	1893 : 16–17
1896	*Bothrioc. claviceps*	Ariola	1896 : 280
1899	*Bothrioc. claviceps*	Lühe	1899 : 43
1900	*Bothrioc. claviceps*	Ariola	1900 : 393
1902	*Bothrioc. claviceps*	Fuhrmann	1902 : 441, 447
1910	*Bothrioc. claviceps*	Lühe	1910 : 25

Specific diagnosis: With the characters of the genus. Large cestodes up to 540mm. long by 2 to 3 wide. Scolex small, elongate, but usually found contracted to an almost spherical shape; 0.5 to 1.5mm. long by 0.3 to 0.5 wide at the middle. Prominent terminal disc. First segments thick, short and crowded; middle, oblong; posterior, or ripe proglottides, usually 2mm. broad by 0.5 to 0.7 long, often quadrate, arranged in groups of two, between which the transverse furrow is not prominent; other transverse furrows well marked.

Cuticula 1 to 2μ thick. Calcareous bodies very scarce. Main longitudinal muscles not in bundles. Four to six chief longitudinal excretory vessels.

No genital papilla; genital cloaca funnel-shaped, midway between anterior and posterior borders of the proglottis. Vagina opens immediately behind the cirrus-sac; no separation between common cloaca and hermaphroditic duct.

Testes large, subspherical, averaging 58μ long, 64 wide and 60 deep; 50 to 60 for each proglottis. Coils of vas deferens loose, close behind uterus-sac, 0.35mm. wide by 0.07 long. Cirrus-pouch ellipsoidal, 127 to 145μ deep by 81 to 104 in diameter, thin-walled.

Ovary compact, 0.45 to 0.55mm. in width, 0.055 in length and 0.18 in depth; isthmus quite thick, ventral. Oocapt 30μ in diameter. Vitelline follicles not separated into two fields on either surface, 450 to 720 in number, 45, 80 and 85μ in length, width and depth, respectively; vitelline reservoir large, 175 by 65μ. Shell-gland posterodorsal, alternating irregularly from right to left opposite the vas deferens. Uterine duct quite voluminous, between ovary and uterus-sac. Uterus-sac transversely elongate, occupying one-third or more of the transverse diameter of the proglottis, usually larger towards the side bearing the opening; openings form a zig-sag ventral row.

Egg, 58 to 63μ long by 37 to 40 wide, without opercula; light in color, show only faintly thru the body-wall.

Habitat: In the pyloric portion of the intestine of the host.

HOST	LOCALITY	COLLECTOR	AUTHORITY	
Anguilla vulgaris		Leeuwenhoek	Diesing	1850 : 590
Anguilla vulgaris	. .	Zeder	Diesing	1850 : 590
Anguilla vulgaris	Rennes	Dujardin	Dujardin	1845 : 618
Anguilla vulgaris	Patavia	Molin	Diesing	1863 : 241
Anguilla vulgaris	Onegasee, Russian Finland	Kessler	Schneider	1902 : 17
Anguilla vulgaris	Sinus Codani; L. Holland, Sweden	Olsson	Olsson	1867 : 56
Anguilla vulgaris	Venice	Ninni	Stossich	1891 : 8
Anguilla vulgaris	Ostsee, Warnemünde and Unterwarnow-Rostock	Braun	Braun	1891 : 55
Anguilla vulgaris			Matz	1892 : 109
Anguilla vulgaris	Genova	Parona	Ariola	1900 : 394
? *Anguilla vulgaris*	Nancy	Prenant	Zschokke	1896 : 818
? *Anguilla vulgaris*	Konigsberg and Memel	Muehling	Muehling	1898 : 35
Anguilla vulgaris	Peninsula of Porkala, Finland	Schneider	Schneider	1902 : 15
Anguilla vulgaris	Lake Garda, Italy	Largaiolli	Ariola	1900 : 394
Anguilla acutirostris	Ireland	Bellingham	Bellingham	1844 : 251
Anguilla acutirostris		Siebold, Coll. Brit. Museum	Baird	1853 : 90
Anguilla anguilla	Germany		Luhe	1910 : 25
Anguilla migratoria		Kroyer	Stiles and Hassall	1912 · 124
Muraena anguilla		Borke	Goeze	1782 : 414
Muraena anguilla	Gryphswald	Rudolphi	Rudolphi	1810 . 38
Muraena anguilla		Kais.-konig. nat'l kab.	Leuckart	1819 : 49
Muraena anguilla	Horja, Scania; Lakes Hålen and Refundsjon, Jemtland, Sweden; Bönan, Gulf Bothnia	Olsson	Olsson	1893 : 16
Muraena cassini	Naples	Rudolphi	Rudolphi	1819 : 472
Anguilla rostrata	Chamcook L., New Brunswick	Cooper	Cooper (the present paper)	
Eupomotis gibbosus	Walnut L., Michigan	H. B. Ward	"	"
Gasterosteus bispinosus	Woods Hole, Mass.	V. N. Edwards	"	"

On account of the fact that, according to Rudolphi (1810:31), Müller (1780:208) ascribed four suckers to his *Taenia anguillae*, we must look to Goeze (1782:414) for the first accurate description of the species. Under the name "Der Kolbenkopf, Taenia *claviceps*" he gave the following diagnosis:

"In den Gedärmen eines Aals (Muraena *Anguilla*), worin sie der Graf von Borke gefunden. Nach dem Berichte dieses genauen Beobachters 4 Fuss lang. So lang hat er ihn noch in keinem Fische bemerkt. Mit der Lupe lassen sich die beiden länglichten Saugwarzen an dem kolbenartigem Kopfe dieses Wurms besser, als unter dem Komposito bemerken. Sie sind deutlicher gegliedert, als die Bandwürmer aus den Hechten. Die Endphalangen mit vielen kleinen Knötigen angefüllt. Dies die Aggregate von Eiern, deren sie im Wasser, worin sie aufbehalten wurden, eine unzähliche Menge von sich gegeben hatten. Die Glieder kann der Wurm kurz und lang machen, wie aus der Zeichnung erhellet. Dieses ist also, wie der Graf hinzusetzt, eine besondere Art von Taenien." Gmelin (1790:3078) retained the specific name, *anguillae*, and described the worm as follows:

"T. capite sessili distincto crassiore, articulis oblongis vage torulosis: osculis duobus in uno latere. . . . Habitat in anguillae intestinis, ad 4 pedes longa, capite anterius truncato, articulis 8 proximis longiore, articulis circiter 600, prioribus subquadratis, latitudine longitudinem duplo, posterioribus orbicularibus: latitudine longitudinem octuplo superante." Rudolphi (1810: 38) gave the diagnosis which has been followed by most of the authors since, excepting as regards the position of the bothria:

"*Caput* polymorphum, articulis aliquot proximis simul sumtis longius, cisque crassius, subtetragonum, sub motu saepe utrinque aequale, subovale, plerumque depressum, postice increscens, anticeque non raro margine tumido, untrinque exstante, terminatum. *Foveae* marginales, sive in latere dextro et sinistro (capitis depressi margine) sitae, oblongae, sub motu variabiles, antice plerumque latiores, mox planiusculae, mox magis profundae. Collum nullum. *Corporis* plani et antrorsum angustissimi articuli varii: primi breves; insequentes longiores, tandem subquadrati, quorum singuli antrorsum angustiores, margine postico tumidiusculo, utrinque exstante; articulis ultimus obtusus. Posteriorum margo lateralis alter media saepe parte foramen distinctum habet. *Ovarium* in eorundem articulorum media parte sacciforme, saepe maculam rubescentem refert" or in more condensed form (1810:37; 1819:136):

"B. capite oblongo, bothriis marginalibus, collo nullo, articulis anterioribus brevissimis, mediis oblongis, reliquis subquadratis, margine postico tumido." F. S. Leuckart (1819:49) was unable to find a scolex shaped like that figured by Goeze, but concerning the material he studied he remarked:

"Der Kopf lang, grossentheils fast viereckt, zuweilen auch ganz keulenförmig; bei einigen vorn mehr abgestumpft und der Rand scharf hervorragend. Einige hatten rund um den Kopf über den Gruben eine schmale Vertiefung. Glieder alle viel breiter als lang, sehr schmal, besonders die vorderen, zusammengezogen. Ovarien habe ich an keinem Examplare wahrnehmen können." While Nitzsch (1824:97) added, erroneously, " . . . die Geschlechtmündungen am Seitenrade," Bellingham (1844:251) merely listed the worm from the eel as above recorded. Dujardin (1845:618) made valuable additions to the descriptions of the species but Diesing (1850:589 and 1863:241), Baird

(1853:89), Olsson (1867:56) and Carus (1885:120) did little more than list the worm in their various works; so that it remained for Matz (1892:108) to give the first comprehensive description of the anatomy, particularly of that of the reproductive organs. Later, apart from reports by various workers of the finding of the species, Olsson (1893:16) noted the infrequent occurrence of the worm in the host, an increase in the number of segments by means of transverse division and the variable form of the scolex; Ariola (1896:268, 272, 273, 280; 1900:393), Lühe (1899:43), Braun (1900:1676) and Fuhrmann (1902: 441, 447) dealt with it from a systematic standpoint; and finally Lühe (1910:25) gave a short diagnosis, mostly after Matz, in placing it in his latest classification of the Pseudophyllidea.

According to Dujardin this species ranges in length from 25 to 540mm. (Zeder), but Lühe (1910:25) gave the length, presumably of average individuals, as from 100 to 200mm. with a breadth of about 2mm. While the specimens from *Anguilla rostrata* examined by the writer were quite small, fragmentary, immature and much elongated, the longest piece, however, not exceeding 20mm., two from *Eupomotis gibbosus*, measured 155mm. in length by 2.9 in maximum breadth, and were much contracted, as indicated in figure 19 of the scolex. The latter, according to the authors, varies in preserved material from an almost spherical shape, as mentioned by Goeze and Leuckart and shown in the latter's Fig. 28, Taf. II, to the much elongate form shown in Matz's Fig. 16, Taf. VIII. The tip of the organ may be protruded, flattened or even replaced by a shallow groove which passes from bothrium to bothrium in the sagittal plane, depending on the degree of contraction or relaxation. These differences are brought out here in figure 23, the latter being more like that of Matz. In either case a slight notch is to be seen on the surficial edges of the terminal disc, while the bothria are deeper immediately behind these than posteriorly where they pass insensibly on to the base of the scolex. The segments have been variously described, but Rudolphi's (1819:136) mention of " . . . articulis anterioribus brevissimis, mediis oblongis, reliquis subquadratis, margine postico tumido" may be considered as indicating their condition in average states of contraction. Matz stated that "Die gleich hinter ihm [the scolex] beginnenden Proglottiden sind, wenn nicht contrahiert, ein Viertel oder ein Fünftel so lang als der Scolex. Die geschlechtsreifen Glieder sind 2mm. breit und ein halb bis drei Viertel mm. lang; man bemerkt an den Gliedern häufig sekundäre Teilung, wie bei *B. punctatus* dadurch wohl bewirkt wird, dass der Rand des vorhergehenden über das nachfolgende Glied sich nicht erhebt, höchstens deutet eine rings herumgehende Furche die Grenze an, wie es auch bei *B. punctatus* der Fall ist;" while Lühe (1910:25) said "Die letzten Proglottiden nahezu quadratisch oder sogar länger wie breit." In the material from *Eupomotis gibbosus* all of the anterior proglottides were found to be much broader than long, on account of the contraction of the strobilae, while those in detached pieces were from four to five times as broad as long, as shown in figure 72. Apart from Matz, Olsson (1893:16) and Lühe (1910:25) have noted secondary division of segments, or as Olsson stated the case, "Hos denna art

framträder mycket tydligt och allmänt en förökning af lederna genom tvärdelning; man finner nästen hvarje led genom en svagt framträdande tvärlinie deladt i två lika led, hvartdera med hanliga och honliga organ, om moderledet haft sådana. Äfven die könlösa leden visa samma förökningssätt," which, however, is what Dujardin observed in 1845 when he said that "On remarque en ontre que souvent les articles sont tellement unis deux à deux, que chaque couple parait n'en faire qu'un seul avec une vide transverse et deux appareils genitaux, l'un devant l'autre." This pairing of the ripe proglottides, also shown here in figure 72, is due to the manner of segmentation which is like that described for *B. scorpii*, only quite regular, since the reproductive rudiments appear relatively farther forward in the strobila and seem to be more stable in development. Concerning this method of increase in the number of segments for this species Lühe (1910:25) said, "Zwei aufeinanderfolgende Genitalsegmente äusserlich häufig nur unvolkommen geschieden, indessen fehlen durchgehende Querfurchen auf den Flächen nie auf so weite Strecken wie bei *B. punctatus*." On account of the great degree of contraction of the only two strobilas provided with scolices at hand, the primary segments were not followed with entire satisfaction very far beyond the scolex, but the first two were seen to be divided into four subsegments each—the first one, shown in figure 19, including the four segments to the * at the side of the figure—with some indication of the next division which would result in eight to the primary segment; the third into eight, and so on. There were indications posteriorly, however, that the primary segment consists of at least 32 genital segments or proglottides, but as in *B. scorpii* the furrows separating sets of 16, 8 and 4 genitalia become almost as prominent as those between the groups of 32, while even those separating pairs are not as faint as Olsson (1893:16) stated and showed in his Fig. I, Tab. II. At all events it should be emphasized that the furrows are more distinct and consequently the proglottides better defined, at least externally, than in *B. scorpii*. In the material studied the segments quickly broaden behind the scolex to 2mm. at a distance of 20mm. from the latter, and then very gradually attain the maximum width. The following table gives the measurements of the three largest specimens at hand:

Length of strobila	155mm.	150mm.	43mm.
Maximum breadth	2.9	2.9	2.0
Length of scolex	0.44	0.46	0.46
Breadth of terminal disc	0.22	0.20	0.22
Breadth at middle	0.28	0.30	0.33
Depth of terminal disc	0.20	0.20	0.20
Depth at middle	0.26	0.20	0.40
Depth posteriorly	0.27	0.27	0.46
Width of ripe joints	2.0		1.6
Length of ripe joints	0.40 to 0.50		0.4 to 0.6

The cuticula, between only 1 and 2μ in thickness, is difficult to distinguish from the finely matted and comparatively dense cuticular musculature. The

subcuticula is from 25 to 40μ deep, and the nuclei of its cells are confined to their central halves. No calcareous bodies were seen in the rather fine-meshed parenchyma, altho according to Braun (1896:1262) such were found by Küchenmeister in this species.

The musculature is comparatively weakly developed. The frontal fibres are fine, scattered thruout the medulla and between the longitudinal fibres; while the same may be said of the sagittal series. The longitudinal fibres are comparatively few and widely separated from each other, and as stated by Matz, "are not arranged in bundles."

The chief nerve strands, about 17μ in diameter, are situated distinctly dorsally in the medulla and between the lateral quarters of the transverse diameter of the segment.

Matz described two main excretory vessels, between which is located the nerve strand, on each side of the body, while Dujardin had previously stated that there were four on each side. In the sections made three were seen to follow a constant course on each side, the nerve strand passing between the more median pair. They are shown in figure 85. The medianmost pair are greatly flattened as they pass close against the uterus-sac somewhat ventrally.

Up to the time when Diesing (1863:241) incorrectly described the genital apertures as marginal and alternating, the only references to the reproductive organs of this species were to the uterus-sacs which, being gorged with eggs in the posterior segments, could be seen thru the thin body-wall in the medial line. Carus (1885:120) failed to correct Diesing's error, so that it remained for Matz (1892:109) to give the first and apparently only adequate description of the genitalia, dealing with, however, only the differences between them and those of *B. scorpii*. The earliest traces of the reproductive rudiments appear about 5mm. from the tip of the scolex while the first eggs in the uterus-sacs come at about 55mm. While the opening of the uterus is well towards the anterior edge of the segment, that of the genital cloaca is midway between the anterior and posterior borders. There is no papilla, the opening being a low funnel-shaped depression in which there is no distinction between the external portion of the cloaca and the hermaphroditic duct.

The number of testes as determined directly is from 50 to 60, while their average lengths, breadths and depths are 52 to 63μ, 58 to 70μ and 58 to 63μ respectively. The similar data as given by Matz are: number, 56, size 36 to 47μ. The vas deferens, about 20μ in diameter, forms a mass of open coils, lateral to the cirrus-pouch and posterior to the uterus-sac, thus occupying the opposite side of the median line from that accommodating the bulk of the uterine tube. The whole mass of coils is about 0.35mm. wide and 0.07 long. Entering the base of the sac with a diameter of 8μ, it gradually enlarges until at the cirrus proper it is twice that size. The proximal end of that portion within the pouch, however, is often found enlarged to form a sort of inner seminal vesicle. The cirrus-sac itself ranges in length from 127 to 145μ and in maximum diameter from 81 to 104. Matz gave the measurements as 109 by 64μ. In comparison with that of *B. scorpii* the wall is quite thin and there

is no dense layer of nuclei just within it, as indicated in figure 96, while the retractor fibres and small amount of parenchyma are quite loosely arranged.

From its opening immediately behind the cirrus-sac, the vagina passes downward and backward among the coils of the uterine duct and joins the oviduct at the dorsal edge of the ovary just a short distance from the oocapt. At the middle of its course it is 15μ in diameter. The ovary is from 0.45 to 0.55mm. wide, about 55μ long and 0.18mm. deep, being thus considerably flattened anteroposteriorly. The spherical ova in the isthmus have an average diameter by 13μ. The oocapt is 30μ in diameter, while the oviduct at the point of union with the vagina is often slightly narrower than the vagina, in fact about 10μ. Large right and left vitelline ducts unite in the median line to form the yolk sac which is 175 by 65μ in size. The vitelline follicles with maximum lengths, widths and depths of 45, 80 and 85μ, respectively, number from 450 to 720, or on the average 570 for each proglottis, as calculated by Matz's method. They are not separated into two fields on each surface but strongly united around the reproductive apertures, unlike the *B. claviceps* of Matz, the two ventral fields of which were only weakly united while the dorsal were strongly so. The shell-gland is posterodorsal and on the other side of the median line from the vas deferens. The uterine duct is so voluminous (Fig. 72) that it crowds the uterus-sac and vas deferens to the other side of the median line. It alternates irregularly from right to left, as do the latter. The sac itself is situated in the anterior half of the proglottis where it is somewhat flattened in the longitudinal direction and constantly occupies one-third of the transverse diameter, as shown in Matz's Fig. 15. The openings, each about 30μ wide, form a zig-zag ventral row, since they are not exactly in the median line but as much as 0.3mm. apart. Apart from being somewhat ragged or villous they are not specially noteworthy.

While the eggs of the European form have been given as from 56 to 60μ in length, they were here found to be from 58 to 63μ long by 37 to 40μ wide when measured in the formol in which the specimens were preserved. They are light in color and so do not show thru the body-wall as in *B. scorpii*.

From the above comparison it will be seen that altho the individuals from *Eupomotis gibbosus* (those from which the data were taken) do not exactly agree with the European species, they are sufficiently close to justify their being considered the same. This was made more certain to the writer by the examination of some fragments of the European form, obtained by Professor Ward from Dr. O. Fuhrmann of Neuchâtel, Switzerland, who took them from *Anguilla vulgaris* in "North Germany." But it should be stated that in the latter material the cirrus-sac and ovary are smaller and the uterus-sac much larger, occupying more than half the diameter of the proglottis in many places; or, the reproductive organs seem to become mature relatively earlier, differences in degree of contraction and relaxation being taken into consideration.

The material studied consisted of No. 289 of the writer's collection from *Anguilla rostrata*, Nos. 17.33 and 16.456 from the collection of the University of Illinois, the former from *Eupomotis gibbosus* and the latter from *Anguilla*

vulgaris (North Germany), and No. 17.54 of the same collection from *Gasterosteus bispinosus*.

The most important data of diagnostic value for the two species, *B. scorpii* and *B. claviceps*, are here given in the form of a table for the sake of comparison:

	B. scorpii		*B. claviceps*	
	European data	*Data by writer*	*European data*	*Data by writer*
Length	35-600mm.	677mm.	90-540mm.	155mm.
Breadth	1-7	3.35	2-3	2.9
Length of scolex	0.9-3.0	1.2	0.5-1.5	0.46
Breadth of scolex	0.3-1.7	0.35	0.5	0.30
Breadth of posterior segments	4.0	1.8	2	2.0
Length of same	0.22	0.35-0.85	0.5-0.75	0.5
Number of genital segments per external segment	16	8 or 16	Less than in *B. scorpii*	See text
Number of longitudinal excretory vessels	6, 8, 12	6	4	6
Number of testes	76	30-60	56	50-60
Diameter of same	40.8μ	35-70μ	36-47μ	60-70μ
Dimensions of cirrus-sac	100x50μ	120x80μ	109x64μ	145x104μ
Number of vitelline follicles	490	350-540	462	450-720
Size of same	30-40μ	35-55μ	.....	.....
Arrangement of same	In 2 separate dorsal fields; 2 ventral fields weakly united	Dorsal fields slightly united; 2 ventral fields weakly united	Dorsal fields united; ventral fields weakly united	Dorsals united; ventrals united to same degree
Dimensions of eggs	50-80x40μ	66-80x43-45μ	50-60μ	58-63x37-40μ
Arrangement of uteri	1 row, alternating, or 2 rows	1 row, alternating, or 2rows	.....	.....
Diameter uterus : diam. segment	Only small portion of diameter	1 : 6	1 : 3 - 1 : 2	1 : 3
Longitudinal muscles	Close together	In bundles	Not in bundles	Not in bundles

BOTHRIOCEPHALUS CUSPIDATUS Cooper 1917

[Figs. 24, 25, 69, 70, 86, 102, 106, 107]

1917 *Bothriocephalus cuspidatus* Cooper 1917 : 37

Specific diagnosis: With the characters of the genus. Medium sized cestodes up to 180mm. in length by 2.75 in breadth. Scolex large with very prominent terminal disc deeply notched surficially; bothria long and narrow and quite deep posteriorly giving the scolex when viewed laterally the appearance of an arrow-head; 3.3mm. long, 1.0 wide at middle, 2.5 deep posteriorly. First segments subcuneate and circular in transection, with prominent posterior borders; middle gradually broaden until much wider than long; posterior two to four and half times wider than long, or 1 to 2.7mm. in width by 0.8 in length. Posterior end of strobila usually rounded, even when segments have already become detached.

Cuticula 3.5μ thick, subcuticula 58μ. No calcareous bodies. Longitudinal muscles not in bundles. Four main longitudinal excretory vessels.

Genital cloaca median, halfway between anterior and posterior borders of proglottis, deep and funnel-shaped. Vaginal opening close behind that of cirrus; hermaphroditic duct obscure.

Testes on each side separated into two fields by the nerve strand, inner much narrower than outer; 50 to 60 in each proglottis; 110, 60 and 80μ in maximum width, length and depth respectively. Vas deferens a large compact mass of coils, elongate and lateral to cirrus-pouch, 0.22mm. long by 0.16 in width, alternates irregularly from right to left. Cirrus-sac very large and thin-walled, 0.25mm. in length (depth) by about 0.20 in diameter. Cirrus protruded, 135μ long by 85 in diameter.

Ovary compact, with limbs often turned forward, 0.60mm. wide, 0.10 long and 0.13 thick; isthmus thick. Oocapt 20 to 25μ in diameter. Vitelline follicles 800 to 1000; 70, 50 and 45μ in maximum depth, width and length, respectively; occupying almost the whole of the cortex, strongly united dorsally and ventrally. Common vitelline duct long and narrow. Uterine duct confined to one side of the median line, opposite the cirrus-sac, alternating irregularly from side to side. Uterus-sac spherical, occupying one-third of the diameter of the proglottis; opening median, close to the anterior edge of the latter.

Eggs ellipsoidal, 62 to 66μ long by 42 to 45 wide, oncospheres not developed within uteri.

Habitat: Ceca and intestine of the host.

HOST	LOCALITY	COLLECTOR	AUTHORITY
Stizostedion vitreum (type host)	Flat Rock L., Muskoka, Ont.	A. R. Cooper	Cooper (the present paper)
Stizostedion vitreum	Giant's Tomb Id., Georgian Bay	A. R. Cooper	"
Stizostedion vitreum	Sandusky, Ohio	H. J. VanCleave	"
Stizostedion vitreum	New Baltimore, Mich.	H. B. Ward	"
Stizostedion vitreum	Port Clinton, Ohio	H. B. Ward	"
Stizostedion vitreum	Put-in Bay, Ohio	H. B. Ward	"
Stizostedion canadense	New Baltimore, Mich.	H. B. Ward	"
Stizostedion canadense	Kansas City, Mo.	H. M. Benedict	"
Hiodon tergisus	Havana, Ill.	H. J. VanCleave	"
Hiodon alosoides	Keokuk, Iowa	H. B. Ward	"
"Pickerel"	Gillett Grove, Iowa	G. R. LaRue	"
Percina caprodes	Douglas Lake, Mich.	G. R. LaRue	"
Perca flavescens	Lakes Kegonsa and Monona, Wis.	A. S. Pearse	"

Type specimen: No. 174.2 of the writer's collection.

Co-type: No. 174.3 of the same collection, deposited in the collection of the University of Illinois.

Type locality: Georgian Bay, Lake Huron, off Giant's Tomb Island.

So far as the writer has been able to ascertain a description of this species has not yet been published, nor have any bothriocephalid cestodes been reported for *Stizostedion vitreum* (Mitchill), the common pickerel or wall-eyed pike.

In general appearance this species does not arrest attention until a fairly close examination is made, since it is comparatively small and when much relaxed not so very different, at least posteriorly, from some of the species of Proteocephalus, one of which evidently not yet reported, was found associated with it in the same host. It is medium sized, attaining a length of about 180 mm. with a maximum breadth of about 2.75mm.

The scolex, on account of its comparatively great depth, is more often seen and much more conspicuous from a lateral view (Fig. 25). Dorsoventrally (Fig. 24) it is long and narrow, showing a terminal disc well set off from the bothria, while laterally it is roughly shaped like an arrow-head, as indicated by the specific name chosen, or somewhat comparable to a flask or vase provided with a low conical lid (the terminal disc). The bothria are long, narrow

and elongate oval in lateral view, the greatest depth being near the posterior end. They are separated by a prominent lateral groove on each side, which extends from the anterior edge of the first segment to a dorsoventral groove just behind the disc. The latter itself is deeply notched dorsally and ventrally and on account of this groove quite prominent laterally. It is thus seen that the walls of the bothria are comparatively thin. During life they are quite mobile, as might be concluded from their general appearance as well as from their anatomy. Altho the greatest dorsoventral diameter of both the cavity and the walls is in the posterior portion of the bothrium, the more functional portion would seem to be the anterior part immediately behind the notch of the terminal disc. On account of its powerful musculature the disc evidently greatly assists the relatively thicker walls of the bothria in that region in forming a more powerful organ of adhesion than posteriorly. The thin walls behind would, on the other hand, better assist the sagittal musculature in maintaining suction by presenting a greater surface internally for application to the mucosa of the host's intestine. The measurements of the organ are given in the table below.

The first segments are subcuneate in outline, and show subdivision in a manner similar to that of *B. scorpii*. Each primary segment is divided into two segments of the second order (Fig. 24), and farther back these in turn into segments of the third order, and so on, until in the region where the reproductive rudiments appear the primary segment contains thirty-two subsegments. This plan can be followed as in *B. scorpii* even into the region of differentiation, and indeed much more readily since there is much less irregularity due to intercalated segments and the further subdivision of others. Furthermore, the same sort of dominance of the anterior end of the primary, secondary, tertiary and quaternary segments—that is, until a group of four reproductive rudiments can be recognized—is seen not only in the size of the subdivisions but especially in the first portion of the region of differentiation, in the rate of differentiation of the common rudiment into the different proximal organs of the reproductive system. As soon, however, as the lumina of the uterus-sacs appear, the plan becomes obscured by the gradual enlargement of the posterior borders of the subsegments, even to those of the fifth order. Thus, in turn there may be seen defined, as one follows them backward, groupings of thirty-two, sixteen, eight, four and two sets of genitalia. Eventually, at the posterior end of medium sized strobilas and for considerable stretches of the largest these pairs become separated, so that the segment contains only one set of reproductive organs. These hindermost segments are usually about four and a half times as broad as long, but in the most relaxed strobilas they may be only twice as broad as long. The ripe segments in some cases may be so much elongated and constricted at their ends that they appear barrel-shaped. This accounts for the apparent discrepancy in the measurements of the third and fourth specimens of the table below. As shown (Figs. 25, 69) the anterior part of the strobila has a dorsoventral diameter almost as great as the transverse one—as a matter of fact some parts of the segments are here almost spherical in cross-section—while the

posterior part is comparatively thick and slightly more convex ventrally than dorsally. The strobila as a whole gradually enlarges from the former to the latter.

The following table gives the measurements of six of the largest specimens at hand; all dimensions are given in millimeters.

Length	178	97	66	53	48	38
Maximum breadth	2.74	1.67	1.18	0.72	1.75	1.77
Breadth half way along the strobila	2.04	1.25	0.80	0.64	0.55	1.34
Same immediately behind scolex	0.80	0.26	0.18	0.18	0.18	0.18
Length of scolex	3.35	0.68	1.38	0.83	1.11	1.30
Width posteriorly	0.91	0.26	0.40	0.24	0.37	0.37
Width of terminal disc	1.37	0.31	0.42	0.50	0.44	0.48
Depth posteriorly	2.44	0.27	0.78	0.38	0.60	0.71
Depth of terminal disc	1.16	0.22	0.18	0.26	0.30	0.31
Length of first (primary) segment	1.52	0.15	0.27?	0.14	0.31	0.26
Breadth of same posteriorly	1.03	0.22	0.37?	0.27	0.33	0.31
Length of ripe segment	0.80	0.87	1.14	1.30	0.40	0.61
Breadth of same	2.74	1.67	0.80	0.66	0.51	1.34

The cuticula is very thin, being only 3.5μ in thickness, and with the highest magnifications is resolved into two layers—an outer and an inner, the former about one-half the thickness of the latter, and separated from it by a stratum of granules so minute as to more nearly resemble a membrane. The outer surface of the cuticula is provided with a similar membrane, since there are no cirri or pseudocilia whatsoever. A distinct, tho very thin basement membrane, is also to be seen. The two strata of the cuticula seem to be of pretty much the same consistency since they stain about the same, altho the outer constantly appears somewhat darker at first sight on account of the proximity of its two bounding membranes. On the scolex the outer layer is modified into extremely short and fine spinelets, which, while absent from the terminal disc as well as the posterior borders of the segments, are well developed in the bothria and out over the edges of its walls.

The subcuticula has the usual reticular appearance, is about 58μ in thickness and is provided with numerous comparatively large nuclei (5 to 7.5μ in diameter) distributed equally thruout the tissue, excepting for a stratum about 15μ in thickness immediately beneath the cuticula, which is almost constantly free of them. This outer layer is, of course, composed of the processes of the

syncitial cells below, as well as of other structures lying more deeply in the parenchyma.

The parenchyma shows nothing of particular interest excepting for the comparatively large nuclei of its cells. These are on the average slightly larger than those of the subcuticula, the largest being more constantly about 7.5μ in length. No distinct traces of chalk-bodies were found in sectioned material altho numerous branches of the excretory system resemble such when cut transversely.

The musculature of this species is especially well developed. The frontal fibres, altho rather small, are quite numerous, considerably isolated from each other, and extend from the layer of vitelline glands on one surface to that on the other, everywhere intermingling with the powerful longitudinal series and being discontinuous only where the largest of the reproductive organs are situated. This applies, however, to mature proglottides, for in the segments immediately behind the scolex they are all but absent. In frontal series they are seen to be continuous from segment to segment but naturally slightly more numerous between the sets of reproductive organs, altho they pass freely among the testes. The same description applies relatively to the sagittal fibres. Dorsoventrally they intermingle with the vitelline follicles. On the other hand, the longitudinal series presents quite a marked difference. As a matter of fact the pronounced development of these fibres seems to be an important characteristic of the species. They form an area on each surface in cross-section about 125μ in thickness and consequently so wide as to restrict the cortical and medullary portions of the parenchyma to two narrow regions, respectively about 75 and 90μ in thickness, as shown in figure 86. The individual fibres are large (as much as 6.5μ in diameter), not united into groups as in *B. scorpii* and continuous as a whole from joint to joint. On account of their great number and matted appearance in frontal or sagittal series it was found impossible to determine their exact length; but it may be said that in all probability they do not extend individually for more than one or at most two sets of genitalia along the strobila. Only a weakly developed outer longitudinal series is present, altho the foremost segments have prominent posterior borders, as shown in figure 24. What might at first glance be considered as such, are the very large and numerous longitudinal cuticular fibres forming a comparatively wide area outside of the subcuticular nuclei in the anterior end of the strobila (Fig. 69).

As might be expected from the external appearance of the structure the musculature of the scolex is well developed. Powerful sagittal and radial fibres pass for a short distance behind the terminal disc, which region is therefore, as noted above, the most functional portion of the bothrium. At the middle of the scolex, however, only the sagittal series is very prominent, while posteriorly at the thickest part of the organ, these too disappear almost entirely. The same diminution of the coronal series from in front backwarks is to be seen, although they are at no level nearly so prominent as the other two sets. As in the strobila the longitudinal fibres are very numerous. They pass uninter-

ruptedly into the base of the scolex as two narrow and very thick, dorso-ventral bundles, somewhat trapezoidal in cross-section, and attach for the most part as far forward as the terminal disc to the walls of the bothria in the usual oblique manner. Only a very few pass on to the tip of the scolex. As might be gathered from the prominence of the edges of the terminal disc, its longitudinal arcuate fibres are also very well developed, and obviously essentially related to the greater power of adhesion of the anterior part of the bothrium on each face of the scolex.

The nervous system consists of two chief strands, from 30 to 35μ in diameter, passing thruout the strobila at the junctions of the lateral three-fourteenths with the median four-sevenths of its transverse diameter. These proportions are, however, in other parts of the strobila (especially anteriorly), or in different strobilae, depending on the degree of contraction, often more nearly 1:3:1. They are moreover usually nearer the dorsal surface of the medulla than the ventral. This is on account of the fact that their course is much interfered with by the testes, both having only a limited space in which to accommodate themselves. They pass into the scolex close together—their axes actually about 70μ apart—and then very gradually diverge, only to start to converge again about two-fifths of the length of the scolex from its tip. After diminishing very slightly in diameter each enlarges into an anteriorly truncated ganglion, united with its fellow of the other side by a single commissure which is bent slightly forward into the tip of the terminal disc. The anterolateral edges of the ganglia are at once split into two comparatively large nerves which pass out directly to the edges of the disc and at right angles to the longitudinal axes of the chief strands. This arrangement gives these anterior connections of the nerve strands a very characteristic appearance both in transverse and frontal sections.

The main longitudinal channels of the excretory system are at least four in number, only two of which, however, are at all constant in course, if not in size. These occupy a ventral position thruout the strobila, while the remaining vessels, two or more in number and connected by numerous and irregular branches, are more dorsal in position. In the foremost segments the ventral vessels are comparatively close together and situated considerably within the nerve strands, i.e., towards the median line (Fig. 69). There they vary from 13 to 15μ in diameter, the dorsal vessels having diameters as much as 18μ. As all of these main vessels pass backwards in the strobila they diverge considerably, and become more and more irregular in course as the reproductive rudiments are neared. The ventral vessels, however, remain more constant in course. In the anterior part of the proglottis they pass just outside of the vas deferens on one side and the uterine duct on the other, while in the posterior region of the genital segment they skirt the edges of the ovary or in many cases pass beneath them. They may attain a diameter of 40μ. Furthermore, while the dorsal vessels are forming a very open plexus by numerous large transverse connections in the lateral portions of the medulla, the ventral pair give off at right angles to their courses many short lateral branches passing among the

testes and other median connections more numerous between the sets of reproductive rudiments. In mature proglottides only the more regular ventral vessels can be followed with any degree of satisfaction. As the vessels enter the scolex, the dorsal series soon breaks up into an irregular plexus, consisting of large branches and lacunae, situated more particularly in the large posterior portions of the organ; while the ventral pair quickly diminish in size and regularity of course, but do not lose their identity entirely until at least one-half the length of the bothria is passed. In the youngest strobilas at hand what was considered to be the "end proglottis" showed the excretory system as terminating in an irregular plexus from which numerous foramina secundaria passed to the exterior quite as in Fraipont's (1881, Fig. 8, Pl. II) view of the conditions in *B. scorpii*.

The genitalia have the general habit of the genus. The common genital opening or cloaca, situated dorsally in the median line, is usually about half way between the anterior and posterior borders of the proglottis, while the uterus opening on the ventral surface is quite near the anterior border, so close in fact that in much contracted strobilas it may be all but obscured by the posterior border of the proglottis ahead. Unlike *B. scorpii* both openings are situated at the bottom of comparatively deep depressions, as shown in figure 102, that of the genital cloaca being usually circular in outline, about 0.10 mm. in diameter and 0.11 in depth. In some proglottides, however, it may be so contracted longitudinally as to present a transverse diameter of 0.45mm., with a length of only 0.04 and a depth of 0.13. The ductus hermaphroditicus or secondary cloaca is very shallow in this species, and only about 55μ in diameter. In most of the preparations made it was usually occupied by the tip of the cirrus, when the latter was not extruded, the opening of the vagina forming a very narrow crescent-shaped slit close behind it. In some cases, however, both the cloaca and the ductus were so contracted longitudinally that the tip of the cirrus was found almost inserted into the entrance to the vagina. From this fact, together with the comparatively great depth of the cloaca in such states of contraction, it is conceivable that self-impregnation may take place; but nothing in the nature of a cloacal sphincter to assist in this function is present.

The testes are continuous from proglottis to proglottis in two lateral fields separated by the median row of proximal organs of the reproductive system. Since dorsoventrally they occupy almost the whole diameter of the medulla, each is further separated into two more or less irregular fields by the nerve strand. The more median field consists of little more than one longitudinal row of the follicles. The number of testes is usually from 25 to 30 on each side, with a variation of a few in either direction, thus making the total number from 50 to 60 on the average. They are ellipsoidal in shape with their longest axes transverse to that of the strobila, and attain dimensions of 0.110mm. in width (in the transverse direction), 0.060 in length and 0.080 in depth. On account of their large size, as compared with that of *B. scorpii*, they are naturally much more regularly arranged in the proglottis.

The vas deferens forms a very compact mass of coils lateral to the cirrus-sac and extending from the uterus-sac ahead to the wing of the ovary on that side behind. It alternates irregularly from right to left, as does the greater part of the uterine tube which occupies a similar position on the other side of the cirrus-sac. In states of moderate contraction of the proglottis it is about 0.22mm. in length, 0.16 in width and 0.18 in depth. Immediately within the cirrus-sac the vas deferens continues as a thin-walled seminal reservoir, slightly coiled and occupying approximately the ventral one-third of the former. It varies from 35 to 80μ in diameter, but in the sections made it was found to contain only a comparatively small number of spermatozoa. Beyond this receptacle the duct narrows down to about 5μ in diameter and continues as the ductus ejaculatorius with many coils, situated in the proximal one-third of the sac alongside the seminal reservoir even when the cirrus is protruded. This portion of the duct very gradually enlarges as its circular muscle fibres become more numerous and its lining thicker and thicker as it merges into the cuticula of the cirrus proper. The latter is about 5μ in thickness and deeply "cleft," or, to be more precise, broken up into a great number of coral-like villi by means of irregular separate pittings reaching almost to the base of the tissue. The duct may here (at the middle of the cirrus-sac) attain a diameter of 25μ. The cirrus proper is somewhat conical when protruded (Fig. 102) and has a maximum length and width of 130 and 85μ, respectively. However, on account of the similar structure and large diameter (25μ) of that part of the duct still invaginated within the sac one is led to think that the organ may reach a much greater length—with probably a considerably smaller diameter. From the tip of the cirrus to the inner end of its duct, where the cleft cuticula stops and which point might well be the functional tip of the organ, it is at least 0.28mm. in length. Thus it would seem that the organ functions as a very efficient and powerful intromittent organ. The cirrus-sac is ovoid in shape and comparatively large, being about 250μ in depth (length of longitudinal axis, which is directed dorsoventrally), 180μ in length and 210 in width, when the cirrus is not protruded, and thus somewhat flattened in the longitudinal axis of the strobila. Its wall is only about 2.5μ in thickness, and composed of very fine muscular fibres the direction of which was not determined with certainty. The contents of the sac consists of a loose parenchymatous tissue, containing many nuclei and numerous retractor muscle fibres. The nuclei, which are situated close around the duct and are comparatively numerous, are in all probability myoblastic in their nature. The retractor fibres pass obliquely upwards and inwards from all points of the wall to their points of attachment to the cuticula of the cirrus. This attachment is seen very nicely when the cirrus is protruded (Fig. 102), for then the fibres are much elongated and theycan be followed even to the evaginated cuticula. Their myoblastic nuclei are quite easily distinguished, especially in the everted portion of the cirrus. The cirrus-sacs are all in the median line, their longitudinal axes being almost constantly in the median sagittal plane.

The vagina opens immediately behind the cirrus at the bottom of the genital cloaca with an aperture which forms an arc of a circle. It passes ventrally in the median line close to the posterior wall of the cirrus-sac and then, after taking a few coils on a level with the lower border of the isthmus, it joins the oviduct a short distance from the origin of the latter. Thruout its course it is considerably flattened anteroposteriorly, its dimensions being alongside the cirrus-sac about 46 by 18μ. It is provided with a cuticula, 3μ in thickness and thrown into longitudinal folds. It gradually diminishes in size until a diameter of about 15μ is reached—at the ventral border of the ovary—and then enlarges somewhat before joining the oviduct in a dorsoventral transverse plane, but without forming a distinct receptaculum seminis, altho a considerable length of this portion of the duct is often found filled with spermatozoa. Unlike that of *B. scorpii* the ovary of this species is a compact organ, 0.60mm. wide, 0.10 long (the wings) and 0.13 deep. The elongated oval shaped wings (Fig. 86), usually directed forwards, since the whole organ is situated right at the posterior border of the proglottis and close against the uterus-sac of the next proglottis, are attached by narrow necks to the somewhat wider and bulbous isthmus. Ova from the latter are oval in shape, measure about 15 by 12μ and have nuclei 6μ in diameter with nucleoli 2.5μ. As in *B. scorpii* the wings occupy the whole of the dorsoventral diameter of the medulla, while the median bulbous portion of the isthmus almost reaches the same level dorsally. The oviduct arises dorsolaterally from the isthmus in the somewhat elongated oocapt which has a diameter of 20 to 25μ and a length of from 25 to 30μ. Immediately beyond the oocapt it gradually enlarges from a diameter of 7 to 20μ where it is joined by the vagina only a short distance either to the right or left from its point of origin. At the junction of these two ducts there is only a very small vestibule, as in the foregoing species, into which, nevertheless, the oviduct may be seen to open by a longitudinal slit, and from one corner of which it proceeds with a diameter of 6.5μ. After continuing almost directly dorsally with only a few very open coils it is joined at about the level of the upper edge of the isthmus by the common vitelline duct. Thruout its course the epithelium of the oviduct is poorly provided with cilia and is surrounded by only a comparatively small number of circular muscle fibres. The common vitelline duct has a diameter just beyond its point of origin with the oviduct of 25μ or more. It is directed transversely above the generative space from the dorsal edge of one horn of the ovary to about the median line, where the separate vitelline ducts unite. In sections it is usually filled with yolk cells. The vitelline ducts, themselves, pass laterally close in front of the wings of the ovary, and hence between them and the vas deferens and uterine tube. When empty, they have a minimum diameter of only 3μ. The vitelline follicles, as shown in figure 86, occupy almost the whole of the cortical parenchyma between the longitudinal muscles and the nuclei of the subcuticular cells. They are ellipsoidal in shape, their longest diameters being directed at right angles to the surface of the strobilia. They are longest near the median line and smallest at the edges of the strobila. In general they may be said to be arranged in two

lateral fields continuous from proglottis to proglottis, but the latter are united dorsally and ventrally between the sets of genitalia by the largest which are somewhat more numerous and irregularly arranged ventrally. The average maximum depth, width and length, of the individual follicles are 70, 50, and 45μ, respectively, while the diameter of the smallest lateral follicles, more nearly spherical in shape, is about 25μ. Their number as calculated from sections averages from 800 to 1000 for each set of reproductive organs. The shell-gland is situated dorsally and to one side of the median line, the beginning of the uterine tube occupying the other side of the generative space. The latter is here not so much a space enclosed by the ovaries as the region of union of the proximal portions of the generative ducts. That part of the oviduct with which the cells of the gland are connected is only about 60μ in length. Beyond the ootype the oviduct gradually enlarges as it passes to the other side to become the uterine tube. Farther ventrally the comparatively large coils of the uterine duct pass back to the same side again and occupy a space lateral to the cirrus-sac, as mentioned above in connection with the vas deferens. Just beyond the shell-gland, where the syncitial nature of its epithelium can be made out, the oviduct has a diameter of 13μ. The uterus-sac is relatively large in this species, spherical in shape and occupies one-third of the diameter of the proglottis anteroposteriorly as well as laterally. This applies to proglottides in moderate state of contraction, for in much relaxed ones it is somewhat ellipsoidal in shape with its long axis in the median line. The youngest uterus-sac which was seen to contain eggs in the largest and most relaxed strobila at hand was spherical and had a diameter of 0.15mm., while the largest of the same chain, also spherical, was 0.50mm. in diameter. But even when they appear circular in outline from a superficial view, they are not in reality spherical since they lead off funnel-wise ventrally to the uterus-opening. The superficial aspects of the latter have been already dealt with above, so that it will be necessary to state here only that it has quite the same structure as that of *B. scorpii*, and that the actual aperture when formed is irregularly circular in outline with a transverse diameter of 60 to 85μ. The wall of the uterus-sac just within the opening is in many cases broken up into numerous processes, evidently cuticular in their nature, which protrude thru the aperture.

The egg is ellipsoidal in shape during life, and from 62 to 66μ long by 42 to 45μ wide. None were found to contain oncospheres, but only masses of cells such as shown in figures 106 and 107, the smaller of which obviously represents an earlier stage in the division of the latter. While most of these cells are yolk-cells, the large one shown at one end of figure 106 is the undivided egg. The granules of figure 107 are those resulting from the breaking down of the yolk-cells. Eggs sectioned in the uterus-sac showed similar stages in development and confirmed these statements. These measurements and drawings were made on August 2, 1912, so that it is probable that the development of the oncosphere is completed in autumn.

Concerning the life-history of this species it may be said that many of the earliest formed segments are lost long before they become sexually mature,

since most of the youngest strobilas were found lacking the end proglottis. Constrictions at about the middle were present in many of them, as if the length of segments behind that region might be thrown off as a whole. Since, however, this is not a constant feature, it is considered to be due rather to the fixation of a wave of contraction passing over the strobila, such as may be seen in living individuals as well as in plerocercoids of other genera of cestodes, e.g., *Scolex polymorphus*.

From the foregoing description it is to be seen that this species of cestode is new. The specific name, here chosen, has reference to the peculiar shape of the scolex as seen from the side: *cuspis*, an arrow-head.

The material studied consisted of Nos. N.B. 6a, N.B. 6d, N.B. 6g, No. 47, No. 50a, No. 54c and P.B. 2 from *Stizostedion vitreum*, N.B. 38a, 08107, 08108, 08109 and 08110 from *Stizostedion canadense*, and Ha 34a and Ha 35a from *Hiodon tergisus*, in the collection of the University of Illinois; Nos. 398, 423 and 481 from *S. vitreum* in the collection of Dr. H. J. Van Cleave; Nos. 7b from *Percina caprodes* and 421 from a "Pickerel" in the collection of Dr. G. R. LaRue; twelve toto preparations from *Perca flavescens* in Dr. A. S. Pearse's collection; and Nos. 41, 170, 172, 173, 174, 193 and 194 from *S. vitreum* in the writer's collection. The material from *Perca flavescens* was larval, while that from *Percina caprodes* was mature but of a small size.

BOTHRIOCEPHALUS MANUBRIFORMIS (Linton 1889)

[Figs. 26, 27, 62, 73, 87, 88, 97]

1889	*Dibothrium manubriforme*	Linton	1889 : 456
1890	*Dibothrium manubriforme*	Linton	1890 : 728
1898	*Dibothrium laciniatum*	Linton	1898 : 425
1898	*Dibothrium manubriforme*	Linton	1898 : 429
1899	*Bothriocephalus laciniatus*	Lühe	1899 : 43
1900	*Bothriocephalus manubriformis*	Ariola	1900 : 410
1901	*Dibrothrium laciniatum*	Linton	1901a : 437
1901	*Bothriocephalus histiophorus*	Shipley	1901 : 209
1902	*Bothriocephalus manubriformis*	Porona	1902 : 7

Specific diagnosis: With the characters of the genus. Large cestodes up to 220mm. in length by 5mm. in maximum breadth. Scolex large, elongate, with prominent terminal disc deeply notched laterally as well as surficially, constricted posteriorly; length 2 to 3.5mm., depth at middle, 1.0, breadth of disc, 1.0. Bothria long and very narrow posteriorly where the walls are quite thick. First segments cuneate with salient posterior borders which are distinctly emarginate; middle, broadly cuneate, less emarginate; posterior or mature, many times broader than long and closely crowded, 5 by 0.2mm.; gravid proglottides, 2 by 0.4mm. Posterior half to two-thirds of the strobila provided with a median line (the combined uterus-sacs).

Cuticula 4.5μ thick. Calcareous bodies large, 18 to 26 by 11 to 15μ. Longitudinal muscles well developed, in bundles. Anteriorly four chief excretory vessels.

Genital cloaca median or slightly displaced towards either side, deep and narrow, separated from hermophroditic duct by a narrow velum, half way between anterior and posterior borders of the proglottis. Vagina opens immediately behind cirrus or very slightly to one side.

Testes ellipsoidal in shape, 64 to 75μ wide, 45 to 60 long, 64 to 80 deep; 60 to 70 in number, dorsal in the medulla. Vas deferens closely applied to inner end of cirrus pouch, 85μ long, 175 wide and 400 thick, somewhat crescentic in the dorsoventral-transverse plane, opposite the uterus-sac. Cirrus-sac long and cylindrical, 0.50 by 0.14mm., inner half deflected towards the vas deferens, walls very thick, composed mostly of circular muscles. Cirrus short, usually not extending outside of the proglottis, 30 to 35μ in diameter.

Vagina with bulbous sphincter near its opening, 50μ long by 70 in diameter. Ovary irregularly branched but compressed anteroposteriorly, 0.45mm. wide; isthmus only ventral. Oocapt 30μ in diameter. Vitelline follicles extremely numerous, 35μ long, 60 wide and 85 thick. Vitelline reservoir large, 60μ in diameter. Uterine duct voluminous on both sides of the median line, crowding all other organs. Uterus-sacs alternate irregularly from side to side, each 0.45mm. in diameter, encroach greatly on neighboring segments, with thick musculo-glandular funnel-shaped ventral portion. Apertures form two lines on the ventral surface 1mm. apart.

Eggs 58 by 34μ, dark brown, showing thru walls ofuterus-sacs.

Habitat: Intestine of the host.

HOST	LOCALITY	COLLECTOR	AUTHORITY	
Tetrapterus albidus (type host)	Woods Hole, Mass.	Linton	Linton	1889 : 458
Histiophorus gladius	Newport, R. I.	Linton	Linton	1890 : 731
Tarpon atlanticus	U. S. N. M.	.....	Linton	1898 : 435
Istiophorus nigricans (=*H. gladius*)	Woods Hole, Mass.	Linton	Linton	1901 : 448
Tetrapterus imperator (=*T. albidus*)	Woods Hole, Mass.	Linton	Linton	1901 : 447
Histiophorus sp.	Indian and Pacific oceans	A. Willey	Shipley	1901 : 209
Tetrapterus belone	Portoferrajo, Id. Elba	Damiani	Parona	1902 : 7

Type specimen: No. 4711, Coll. U. S. National Museum.
Co-type: No. 16.461, Collection of the University of Illinois.
Type locality: "Penekese?"

Although this species was first described more or less in detail by Linton (1889:456) and further notes were added by the same worker in the following year (1890:728), the writer feels that there is still much to be learned about it in spite of the fact that Ariola (1900:410) was able to indicate the genus to which it belongs and to correct some errors concerning the arrangement of the

bothria in his rather brief description, which is inadequate for diagnostic purposes. Consequently an attempt is here made to better define the species so far as can be done with the poorly preserved alcoholic material referred to immediately above.

In general appearance the worm arrests attention on account of the very closely arranged posterior genital segments, which give that part of the strobila a transversely plicate aspect. On closer view the anterior segments with their "salient" posterior borders and the characteristic scolex are seen (Figs. 26, 62). The latter was described by Linton as follows:

"Head cuneate, tetrangular, truncate in front, tapering posteriorly into a cylindrical neck-like part near posterior, then expanding so that the posterior end of the head resembles one of the anterior segments of the body. The general appearance of the head when viewed laterally [surficially] is therefore somewhat like a ball-bat, the constricted part representing the handle. Two longitudinal fossae [bothria], laterally placed, extend from the anterior part of the head to the constricted part. Each of the marginal lobes thus formed is indented at the anterior extremity by a short but deep [only in much contracted material] secondary fossa, which together with the two lateral fossae, give the head when viewed in front a four-lobed appearance. The edges of the lobes bordering the lateral fossae [the walls of the bothria] are thin-lipped and flexible; anteriorly there is a transverse elevation forming both a lateral and a marginal rim and making an obtuse angle between the front and the side of the head." This is the pyramidal or somewhat conical terminal disc, so characteristic of the scolex. (Figs. 26, 27). The walls of the bothria are "thin-lipped and flexible" only when protruded considerably; in moderate states of contraction, that is, nearest to what the writer considered to be the probable state of rest, they are comparatively thick and especially so in the posterior half of the scolex where in consequence the bothrium is reduced to a narrow vertical slit. "The marginal lobes, when at rest, have a rounded outline, fullest in the middle, tapering posteriorly, appressed slightly anteriorly, and raised into two small eminences on each side of the secondary fossae. The head in a marginal view is somewhat flask-shaped. Seen from the front the head is squarish, with the angles rounded and the sides deeply cleft, the clefts rounded, the lateral clefts deeper than the marginal."

As regards the segments Linton in continuation stated that: "Immediately back of the head the segments are very narrow, and for a greater or less distance, depending on the state of contraction, maintain about the same width as the base of the head. In some individuals the small anterior segments continue much farther back from the head than in the one figured. The segments are alternately short and long. This characteristic is quite plainly marked in the segments which immediately follow the head, is still noticeable on the median segments and also on the posterior ones, but is not so plainly marked on the latter as on the two former." This is due to the manner of subdivision of the segments which is carried out in the same way as in *B. scorpii* and *B. cuspidatus*. It can be followed with certainty, however, only in the "anterior"

and middle portions of the strobila and not posteriorly where the segments are very short and crowded close together longitudinally, even tho the latter may not show the rudiments of the reproductive organs. Figure 62 is an outline of a primary segment, the fifth from the scolex in this case, to show this method of subdivision. Dominance of the anterior over the posterior half of the segment as regards rate of division is well shown; and this is seen to be applicable also to the subsegments even to those of the fourth order. "In one specimen examined," to continue to quote from Linton, "the first six segments did not show this alternation in size. In the next fourteen segments, however, the alternation was quite evident." This indicates that he noted the division of the segments into subsegments but did not ascertain the exact manner in which it is carried out. "The small anterior segments are terete, subtriangular in outline, narrow in front, wide behind, the length nearly equal to the greatest breadth." It is rather difficult to say to what segments or subsegments the latter part of this statement refers, since it describes not only what is here considered to be the first primary segment, i.e., the largest segment immediately behind the scolex as shown in the figure 26, but also many of the major subsegments of the following primary segments —not all, however, since as indicated in figure 62, the dominance in division mentioned above renders subsegments of the same developmental value different in size. Furthermore, as regards these anterior segments it must be emphasized that their prominent or salient posterior borders are distinctly emarginate, which condition, very obvious in the segments immediately behind the scolex, can be followed back to the region where the segments get very broad and short. Concerning this notching of the posterior border, Linton (1889:458) said: "The segments of the first series are sometimes notched or crenulated on the posterolateral margin, with a single median indentation; in others the edge is but slightly wavy; in others it is nearly entire." In the material at hand, however, this emargination was found as just described in all of the specimens, altho in much contracted strobilae it is at first sight apparently absent. "The succeeding segments are much broader than long. At the widest part the ratio of the breadth to the length is as much as fourteen to one. As the segments increase in width they become much crowded together and thickened. . . . The crowding together of the median segments is not due to contraction, but seems to be a permanent characteristic of the species." Concerning the posterior segments Linton noted further (1890:729) that in the dead specimen taken from *Histiophorus gladius*, actually No. 16.461 referred to above, "The margins of the strobila are apparently entire. The segments are very short, with their posterior edges slightly wavy on the median segments, thus suggesting those of *D. plicatum*. The posterior edges of the median segments are crowded together like the edges of the leaves of a book about 0.2mm. apart. Near the posterior end they are not so closely crowded, being about 0.4mm. apart." (Fig. 73). Confirmatory frontal sections showed that this "entire" nature of the edge of the strobila is in reality due to partial decomposition; yet at the same time the surficial portions of the posterior borders of

the segments did not seem to be much affected. In addition it should be noted that besides being "not so closely crowded" the segments at the extreme posterior end of this strobila are relatively much narrower, as a matter of fact, only two-fifths as wide as the widest part of the strobila. This seems to be quite comparable to the elongation of the posterior end of Schistocephalus when it reaches the final host and matures.

Another important characteristic, which should be mentioned here in dealing with the external features, is that "In alcoholic specimens a dark median line will be noticed extending from the posterior end to the middle or anterior third of the strobila. This is due to the centrally situated ovaries [uterus-sacs] which are crowded with eggs," while "a median furrow on one of the lateral [surficial] faces of the body begins toward the anterior and becomes punctate towards the posterior region, where the minute lateral genital apertures become visible in a zig-zag row."

The following table gives comparative measurements of several strobilas, the first columns being the data given by Linton:

Specimen	1	2	3	4711, U.S N.M.		16 461
				Data by Linton	Data by the writer	
Length of strobila	133mm	140mm	20mm.	115mm.		220mm.
Length of scolex	3 50	3 00	2 10	2,2.5,1 5	2 0	
Breadth of terminal disc	1 00	0 90	0 80	1,1;1 2	0.94	
Breadth just behind terminal disc		0 80	0.60			
Breadth at middle of scolex					0 64	
Breadth at constriction		0 21	0 31		0 44	
Breadth posteriorly					0 81	
Depth of terminal disc					0 89	
Depth at middle		0 90			1 05	
Depth at constriction					0 58	
Depth posteriorly					0 63	
Length of first segment					0 39	
Breadth of same anteriorly		0 42	0 28		0 54	
Breadth of same posteriorly		0 80	0 50		0 89	
Maximum breadth of strobila			0 90	3 5		5 0
Length of widest segments			0 12			
Breadth of posterior end of strobila						2 0
Maximum thickness of same						1 5

Concerning the cuticula little can be said, since the material studied was very poorly preserved. Only in sections of a very young strobila was it seen with any degree of certainty. There it was found to be about 4.5μ in thickness, and divided by differences in degree of staining into a dark outer one-

third composed of very closely set "cirri" and an inner two-thirds, which took the stain with great avidity, leaving only a thin outer lighter part which by its contrast in color with the cirrous stratum served to set the latter off distinctly from the much thicker inner and more homogeneous part. The cuticula was not found to be in any way specially modified on the scolex, altho such might be found to be the case in well-preserved material. It was naturally retained in its entirety only within the bothria.

Only in the smallest strobilae could the subcuticula be made out satisfactorily. It is from 25 to 40μ in thickness, and composed of somewhat conical cells, the inner ends of which are quite cylindrical while the outer are much branched, divergent and interlacing. Hence the cylindrical portions, proximal to the nuclei and usually somewhat smaller in diameter than the latter, are seen to stand out distinctly and quite separately from the much less dense underlying parenchyma. The outer dendritic portions cannot be allotted with certainty to their proper cell bodies on account of this complicated mesh-work which they form just beneath the cuticula, but they can be followed to the cuticula, their attachment to which is readily seen.

Chalk-bodies in the poorly preserved parenchyma are usually elliptical in outline, with maximum lengths and widths of 18 to 26 and 11 to 15μ, respectively. They are fairly numerous and scattered thruout all parts of the strobila, being most plentiful in the cortex of ripe proglottides. In the scolex a very few small ones are to be found only in the enlarged posterior portion of the organ, where they are confined to the medulla, no doubt on account of the great development of the musculature. They are also more numerous perhaps in the medullary portion of the parenchyma of the anterior segments than in the cortical region. In general it would seem that they are developed in that portion of the parenchyma which is little occupied by other tissues or organs, chiefly muscles or genitalia.

The musculature of this species is very well developed and powerful. It was described by Linton (1890:729); but since his description is somewhat difficult to follow, the main features of its arrangement will here be given even at the expense of reporting much that has already been reported.

The frontal series is well developed and consists of two layers on each surface of the strobila, an outer, just outside of the thick layer of main longitudinal muscles, and an inner, just within this or bounding the very thin medullary parenchyma outwardly, as shown in figure 87. In the anterior segments a third series of frontal fibres appears as the posterior flaring border of the segment is approached. It forms a ring around the whole strobila, i.e., connecting with its fellow of the opposite surface laterally, unlike the other two layers, just within the subcuticula or a little more than half way from the outer edge of the layer of main longitudinal fibres to the cuticula. This series as evidently pointed out by Linton, divides just ahead of the bay behind the posterior border of the segment, part of it going to the outer, posterior border and the rest remaining within. While the latter as just indicated does not go far posteriorly, the former passes to the hinder edge of the salient border. In

mature proglottides the layer of frontal fibres just external to the main longitudinal group is greatly thickened close to the posterior border of the segment. There it forms a transverse ropelike strand, no doubt owing in part at least to the numerous vitelline follicles situated in the cortex between these levels. And this statement applies in like manner, but especially more towards the median line of the strobila, to the innermost series of frontal muscles. These, however, are further interfered with chiefly by the uteri and cirrus-sacs.

The sagittal or dorsoventral fibres are quite prominent on account of the fact that they are arranged in bundles which in the anterior segments find their way from the medulla out into the cortex between the fasicles of the main longitudinal series. They are less numerous laterally than medially. In mature segments, on the other hand, they are crowded and somewhat obliterated medially by the large genital organs, and are consequently more numerous laterally, that is, beyond the edges of the uterus-sacs. Longitudinal sections show that large numbers of them pass to the tip of the salient posterior borders of the segments and hence serve to retract the latter.

The longitudinal muscles are present in two groups, an inner, or main, and an outer series. The former appears as a very conspicuous layer of large fibres arranged in fasicles or bundles on each surface of the strobila and occupying one-half or more of the dorsoventral diameter of the cortical parenchyma. The latter are on the average much smaller, less numerous, more dispersed, and situated in the portion of the cortex between the outer frontal fibres and the cuticula. In the anterior segments the layer of inner fibres is about 70μ in thickness in the median line, and thins out gradually laterally where it joins its fellow of the opposite surface by a few fibres which lie in the plane of the flat, ribbon-like medulla (Fig. 87). Linton does not seem to have noticed this lateral union of the two layers, since he said that "It [the longitudinal muscle layer] is, moreover, interrupted at the margins where it is penetrated by the margins of the inner core [the medulla]." Farther back where the segments become very broad and short it averages about 85μ in thickness, while in mature proglottides the thickness amounts to 145μ. At the same time the fasicles, in the anterior segments quite rectangular in outline, the longer diameter being dorsoventral in direction, become more elliptical in transection. In the latter case the individual fibres are circular to elliptical in transverse section and have a maximum diameter of 15μ. In describing this group of longitudinal muscles in "transverse sections made thru that part of the body which is immediately in front of the segments that contain ripe ova," Linton stated that they ". . . are very large, altho not at this point in distinct fasciculi." This was not found to be the case in the sections studied by the writer, since fasciculi were seen all along the strobila even in the base of the scolex, altho it is true that anteriorly they are separated by only a small amount of parenchyma besides the bundles of sagittal fibres passing between them. As regards the other series of longitudinal fibres Linton rightly observed that "the longitudinal fibres of the inner part of the granular layer [here described as the outer portion of the cortex] do not differ essentially from those of the longi-

tudinal muscle layer proper, except that they are more scattered. . . ." Centrally the individual fibres of this group are of the same diameter as the smallest of the main group, while peripherally they dwindle in size as they approach the cuticula to such an extent that there they are indistinguishable from the longitudinal cuticular fibres. Longitudinal sections show that they bear the same relations to the salient posterior borders of the segments as are described here for *Clestobothrium crassiceps* and other species and emphasized by Lühe (1897a). Anteriorly a number of them pass off into the posterior border in the typical manner; but, as might be expected, they are comparatively scarce in the posterior reaches of the strobila. Again, Linton stated that "the longitudinal muscular fibres in general do not lie parallel with each other." This was found to be more strictly applicable to those within the fasicles, since only a comparatively few fibres pass from fasicle to fasicle longitudinally. But, as in other species, they are continuous from segment to segment as are indeed all of the groups of muscles, so that as far as their general arrangement is concerned, Linton's (1890:731) statements are thoroughly justified:

"Longitudinal sections were carried thru several contiguous segments. In these there were no septa to indicate a division of the body into true segments. The only indication of a segmented condition is the superficial character of the projecting posterior edges. The longitudinal muscles are continuous and the ovaries [uterus-sacs] are crowded together so as to form an almost unbroken zig-zag line. So far as any internal characters go, the body is practically continuous."

The musculature of the scolex is especially well developed, the sagittal and radial fibres being very numerous. An unusual augmentation in the number of the former appears towards the outside of the walls of the bothria, extending from the dorsal to the ventral surface. Their exact course is obscured somewhat laterally in the median frontal plane by the interdigitation of the radial fibres which takes place there, that is, opposite the lateral grooves. As the posterior borders of the scolex are approached they diminish in number and size and eventually disappear. Coming into the base of the scolex as an elliptical ring in cross-section with its thickness almost as much laterally as dorsoventrally, the layer of main longitudinal muscles soon sends out dorsoventral horns into the walls of the bothria on each side and becomes arranged in general much as in *Clestobothrium crassiceps*—doubtless an adaptation to the almost closed nature of the bothria. The outer longitudinal fibres are arranged on each side of the scolex as a continuous lateral band between the lateral sagittal fibres just mentioned and the cuticula, and extending from the dorsal to the ventral surface. Each bothrium has a much smaller and thinner band on each side next to the cuticula lining its cavity. The terminal disc is almost completely filled up with very powerful longitudinal arcuate fibres for the protrusion of its edges.

In the anterior segments the two chief nerve strands are situated in the medullary parenchyma between the lateral and median quarters of the transverse diameter of the strobila. From 18 to 30μ in diameter, they fill up the

whole of the medulla dorsoventrally at these points. In mature proglottides they have the same relative positions in the frontal plane, but are located in the ventral one-half of the medulla, their transverse diameter being as much as 50μ. In the scolex each expands opposite the edges of the terminal disc to form a ganglion, which sends out a large branch to each of the two quadrants of the disc on the same side, and connects with its fellow by a slightly narrower commissure.

Four main longitudinal excretory vessels maintain a constant course thruout the anterior segments. These are arranged in two pairs, a more median and a lateral, not in the same plane in the medulla. The members of the latter are the larger and are situated at the sides of the median one-quarter of the transverse diameter of the segment. All of these vessels are connected at various levels by large branches to form an extensive plexus thruout the medulla. In the posterior crowded segments, however, the main vessels become lost in the plexus, altho here and there they seem to occupy their original positions thru a few sections. Only two large vessels, probably the lateral pair, giving off many branches of the same calibre, can be followed with certainty into the scolex. About half way to the summit of the terminal disc they break up into a plexus which ramifies thruout the walls of the bothria. The posterior end of the smallest strobila at hand showed the same sort of communication of a terminal plexus with the exterior thru large side branches and foramina secundaria as in *B. scorpii*.

Linton (1889:457) described the reproductive organs in general in the following words: "In alcoholic specimens a dark median line will be noticed extending from the posterior end to the middle or anterior third of the strobila. This is due to the central situated ovaries [uterus-sacs], which are crowded with eggs. The genital apertures are lateral and may be traced in an irregular zig-zag line on one side from about the anterior third of the body. In the mature segments they are rendered obscure, if not wholly obliterated, by the mass of eggs with which the center of the segment is filled," and later (1890: 729, 730) besides giving the external features, quoted above, stated that "The reproductive apertures are near the median line on one of the lateral sides. They are very close together and rather small. Each aperture represents a pair of sexual organs, cirrus and vagina. Upon making a few longitudinal sections on the lateral [dorsal] face which bears the reproductive apertures, the small vaginal opening comes into view. It opens into the common aperture from behind and near the surface. The large aperture continues into the cirrus-bulb. . . . " Linton correctly stated that the common genital openings are arranged "in a zig-zag row" in the median line, as shown in figure 73; but much of this irregular lateral displacement in the mature proglottides would seem to be due to lateral pressure exerted by other organs, probably the gorged uterus-sacs or at least the uterine ducts, since in immature segments where the cirrus-sacs are already well developed, they are almost exactly in the median line. In sagittal sections the genital cloaca is seen to open to the exterior at about the middle of the length of the very short mature proglottis

and to be in many cases just covered by the posterior border of the segment immediately ahead. It is in the form of a narrow tube, often somewhat enlarged ventrally, with a length of from 85 to 115μ and extending at right angles to the general surface of the strobila. A secondary genital cloaca or ductus hermaphroditicus is present at the bottom of this tube and is separated from the latter by a valve-like muscular extension of its walls (Fig. 88). Behind this the cirrus is often found partially extended and directed backward towards the opening of the vagina or actually in contact with the vaginal sphincter. No sphincter muscle surrounding the genital cloaca at any level was found, altho a number of frontal fibres of the body muscles, curving around the structure both ahead and behind have the general appearance of such a structure. Very early traces of the reproductive rudiments were found in sections of segments 75mm. from the tip of the scolex of one of the largest strobilas studied.

The testes, continuous from proglottis to proglottis, are spherical to ellipsoidal in shape, with their longest axes usually transverse in the latter case. The measurements from sections are as follows: width, 64 to 75μ; length, 45 to 60; depth, 64 to 80. On account of their being closely and irregularly crowded in the very short segments no attempt was made to count them directly; but the average number in the transverse sections (22 to 23) multiplied by the average for each proglottis from sagittal sections of a long series of segments (3 to 4) gave about 67. The correct number is probably between 60 and 70. They are arranged in a layer in the dorsal half of the medulla, where they show some tendency towards stratification. A few, however, were found outside of the medulla, that is beyond the inner frontal muscles and between fasciculi of the main longitudinal musculature.

The vas deferens forms a compact mass of coils, closely applied dorsolaterally to the proximal deflected end of the cirrus-pouch, and alternating irregularly from side to side constantly opposing the uterus-sac. In ripe proglottides it is quite compressed anteroposteriorly by the uterine tube, and also, as a consequence, often extends thruout almost the whole of the medulla dorsoventrally, in which case it is crescentic in outline in transverse sections with the concave side directed towards the median line so as to somewhat surround the cirrus-sac. The average measurements of the mass of coils are: length, 0.085mm; width, 0.175; depth, 0.400. While it was found impossible to measure satisfactorily the size of the duct, gorged with sperms in the mass, it was seen to enter the base of the very muscular cirrus-sac with a diameter of 7.5μ. Within the latter it expands to 15μ and proceeds with this caliber in the form of a compact lot of close and somewhat spiral coils for about one quarter of the length of the pouch. In the second quarter, i.e., from the ventral end of the sac, it pursues a straight course and evidently functions as a quite efficient sperm receptacle since it is here usually from twice to three times as large as before. In the dorsal half of the pouch it again dimishes to from 5 to 7μ and continues still in a straight course to the opening as the cirrus proper. Thruout its whole course its wall is very thin, including only a very

few circular and longitudinal muscle fibres. Distally the cuticular lining is reduced to a minimum. Thus the cirrus when protruded, usually for a short distance only, is a comparatively weak structure with thin walls, but a diameter at the base of from 30 to 35μ. It is also quite short since in no place in the sections made was it found extended more than half way to the external opening of the genital cloaca, but more often, as noted above, turned around in the ductus hermaphroditicus towards the vaginal opening. Thus it is evidently adapted to the function of simply conveying the spermatozoa to the latter orifice in the act of self-impregnation rather than of acting as an intromittent organ in cross-fertilization. The diameter of the retracted cirrus was given by Linton (1890:730) as 0.008mm.

The cirrus-sac is comparatively long and cylindrical and extends from the inner boundary of the genital cloaca to the median frontal plane of the proglottis. While its dorsal half is situated more at right angles to the surface, its ventral half bends over in the transverse plane to the right or left to become related to the coiled vas deferens in the manner described above. This deflection of its proximal end thus alternates irregularly with the latter, and is always away from the uterus-sac. The maximum length and diameter in the latter case in the dorsal half of the organ are 0.500 and 0.145mm., respectively. As shown in figure 88, and as noted by Linton, the walls are very thick, leaving only a comparatively narrow cavity to accommodate the cirrus; they are composed of a very powerful inner layer of circular muscles surrounded by a thin layer of longitudinal fibres which do not have any points of attachment to the body-wall, so far as could be determined. The space surrounding the ejaculatory duct and cirrus proper accommodates the fine and quite long retractor fibres and a small amount of parenchymatous tissue. The retractors are not, however, as large or numerous as in the previous species of the genus in which the cirrus is better developed.

The vagina, which opens close behind the cirrus and usually somewhat towards the same side to which the latter is deflected, begins with a bulb-like sphincter, quite like that described and figured by Linton (1898:436) for his *Dibothrium laciniatum*, 60μ in length by about 90 in maximum diameter. The walls of this structure, 40μ in thickness, are composed of two layers of muscle fibres of equal thickness: an outer of loose circular, and an inner of somewhat radially arranged fibres. The whole organ would thus appear to be adapted to the pumping of the sperms into the vagina. The latter proceeds ventrally with a diameter of about 25μ, after enlarging considerably immediately behind the bulb. It is surrounded by circular fibres only. At the level of the ventral end of the cirrus-sac it joins the oviduct.

The ovary, which has an average width of 0.45mm., is irregularly branched in mature proglottides, much compressed anteroposteriorly by the numerous coils of the uterine tube, and often displaced from the median line by the latter and the spacious uterus-sac. Furthermore, while the isthmus, itself irregular in shape and hence somewhat difficult to distinguish from the rest of the organ, "lies next the inner side of the lateral [ventral] muscular wall," the wings

curve upward on each side, sometimes reaching almost to the dorsal boundary of the medulla. The oocapt is almost spherical in shape with an average diameter of 30μ, and is situated in the median line. The oviduct immediately beyond the narrow outlet of the oocapt is 25μ in diameter. At the point of union of the vagina with the oviduct there seems to be a vestibule, similar to that of *B. scorpii*, but this was not made out to the writer's satisfaction. Two vitelline ducts, each about 15μ in diameter, unite at about the level of the oocapt and continue dorsally with the same diameter as the common vitelline duct. This turns downward again and quickly enlarges to form the vitelline reservoir, which was found to have a maximum diameter, when filled with yolk cells of about 60μ. The vitelline follicles are extremely numerous and very closely arranged in the cortical parenchyma in two lateral fields, a median strip being left free of them on each surface of the strobila. They are ellipsoidal in shape, with average maximum lengths, widths and depths of 35, 60 and 85μ, respectively. In the material studied they showed considerable tendency towards stratification and on account of this fact, their very varying size and the poor condition of their walls, no satisfaction was experienced in attempting to determine the approximate number for each segment; but it must be well over one thousand from a comparison of the sections with those of *B. cuspidatus*.

The uterine duct begins approximately in the median line, quickly expands between the cirrus pouch and the ovary, first in the direction of the coiled vas deferens and as far laterally as the edge of the ovary, and then crosses the median line to the opposite side where the mass of coils, occupying the whole dorsoventral diameter of the medulla, further enlarges gradually in all directions and joins the comparatively large uterus sac. In toto preparations the duct and sac are seen to form a continuous club-shaped mass gorged with eggs and with the larger end, the sac, alternating irregularly from side to side. This irregular alternation of the uterus-sacs was evidently not noticed by Linton since he spoke of only "a dark brown median stripe made by the ripe ova in the crowded ovaries [uteri] "; but Ariola (1900:410) said of them: "Le masse ovariche spesso sono irregolarmente collocate da una parte e dall' altra della linea mediana." Only in sections can one distinguish the sac from the duct, since the two are so closely applied to each other. In dorsoventral view the uterus-sac, itself, is somewhat circular in outline, when not pressed against one of its fellows ahead or behind, and has a maximum diameter of 0.45mm. Ventrally, however, it is funnel-shaped. As shown in figure 73, it may become so enlarged as to invade the adjoining proglottides to a considerable extent. The aperture is located in the middle of the sac and consequently forms with its fellows two lines of irregularly alternating pores on the ventral surface of the strobila, about 1.0mm. apart. It is only about 20μ in diameter, and is situated towards the anterior border of the proglottis, often well under the overlapping posterior border of the segment ahead. The lowermost or funnel-shaped portion of the sac, little more than that which passes through the stratum of longitudinal muscles, is surrounded by a thick layer of material, as shown in figure 97, the nature of which was not determined satisfactorily. It appears

to be glandular in nature, altho muscle fibres traverse the mass in several directions, the inner of them being longitudinal and the outer circularly oblique. Altho this structure may have a glandular function in connection with the passage of the eggs to the exterior, it obviously acts as a powerful sphincter controlling the same and permitting perhaps of the laying of only a few at a time. Distal to the outer end of the funnel, where it loses these fibres, the sac continues through the cortical parenchyma as a narrow tube to the pore.

The eggs of this species were said by Linton (1889 and 1890) to be of two kinds: ". . . one yellowish in mounted specimens with a strong shell, in some cases white and opaque; another sort transparent, with a very thin shell." These differences were seen in the material studied, but they were considered to be merely due to differences of age, the thinner-shelled ones being the younger. While the same author gave the length and breadth as 45 to 54μ and 27 to 30μ, respectively, the writer found their maximum dimensions to be in sections 58 by 34μ.

The material studied consisted of two lots: No. 4711, in the collection of the United States National Museum, from the rectum of *Tetrapterus* sp. from Penekese, determined by Linton; and No. 16.461 in the collection of the University of Illinois, from the intestine of *Histiophorus gladius*, obtained from Prof. Linton, and evidently the actual specimen described by him in 1890. The details of the anatomy, here given, were studied from confirmatory sections of the latter.

DIBOTHRIUM LACINIATUM Linton

Linton (1898:425) established this species on the basis of the material contained in lot No. 4741 of the collection of the United States Museum from *Tarpon atlanticus*, and again reported it from the same host species in 1901 (p. 437). Lühe (1899:43) in his list of the species of the genus Bothriocephalus s. str. remarked that "Von weniger gut bekannten Arten gehören anscheinend noch hierher *Bothriocephalus laciniatus* (Lint.) und *occidentalis* (Lint.);" while Ariola (1900:414) also placed it in the same genus, as he conceived the latter to be constituted.

During the study of *B. manubriformis* the writer was impressed with the great resemblance between *D. laciniatum* and it, in all but a few details, the two being, in fact, identical. The measurements for length and maximum breadth, as shown in the comparative table below, agree, while those of the scolex and anterior segments are as near as can be expected from cestode material which is found in various degrees of contraction and relaxation. All of the conditions represented in Linton's (1898) Figs. 7 to 12, Pl. XXX, were observed in the material of *B. manubriformis* studied—when such obvious errors as, "Fossettes marginal as to head, corresponding to the flat surface of the body," are taken into consideration—while the description of the external features, excepting that of the posterior segments, applied in detail. But later lot No. 4741, U.S.N.M., was obtained by Professor Ward, and the writer

learned that his suspicions were well founded; for *D. laciniatum* proved to be identical with *B. manubriformis*. The posterior segments "with breadth one and a half times the length" had different proportions from those observed in mature material of the latter species, because they were, altho gravid, of quite youngers trobilas. The material of No. 4741 is, in fact, intermediate between No. 4711 of *B. manubriformis* and the 16.461 of the same species dealt with above, not so much in size since it does not show the regions so well, as in degree of maturity. The fact that "the segments are not uniform; one segment with a salient posterior border followed by about two with less salient borders" is due to the irregular manner in which the primary segment divides into subsegments. The dimensions of the eggs correspond, while the measurements of the cirrus-bulb, vaginal sphincter and calcareous bodies are the same in the two species. Linton stated that in *D. laciniatum* "The reproductive cloacae lie along the median line of one of the flat surfaces of the body. The external openings of the uterus lie along the median line of the opposite surface." While the former was found to be the case, the latter was not, for the openings of the uteri lie irregularly on either side of the median line as in *B. manubriformis*. Furthermore, the cirrus-bulb was not found to have "its inner end deflected to the right [left, when we take into consideration the fact that the common genital cloaca of *D. laciniatum* was considered to open on the ventral instead of the dorsal surface] where it communicates with the vas deferens, which lies in numerous folds in front and to the right of the cirrus-bulb," but to alternate irregularly from side to side according as the uterus-sac and distal end of the uterine duct occupy the other side of the proglottis; while the vas deferens was as described above (p. 142). Altho the vaginal bulb was found to be a little larger in the material of *D. laciniatum*, its structure and position were also quite as in *B. manubriformis*. On the other hand no muscle fibres completely encircling both genital apertures, such as shown in Linton's Fig. 5, Pl. XXXI, were seen, but what might easily be taken for such were formed by the crossing of much curved and spread longitudinal and transverse fibres of the body wall, in such a manner that the portions intersecting at the four corners run in almost circular directions and concentrically parallel to each other so as to give the appearance of the whole forming a complete ring in each case. The genital cloaca was found to be shallower than in the material from *Histiophorus gladius*. This is evidently due to the fact that the proglottides were younger and not yet gravid as in those from the latter host. The uterus-opening was not found to be "lined with cilia" but with irregular ragged processes which are evidently only portions of the lining of the developing funnel and the external duct of the same. Finally the position and structure of the ovary, of the vitelline reservoir and of the various layers of the body exactly correspond in the two forms.

Consequently the writer feels that there can be no doubt whatever concerning the identity of *D. laciniatum* with *B. manubriformis*, which fact also seems to be recognized in the Fauna of the Woods Hole Region (Sumner, Osborn and Cole, 1913: 585) where the former is not found among the cestodes, altho

the host, *Tarpon atlanticus*, is listed. Since *B. manubriformis* was described before *D. laciniatum*, the latter must now be considered as a *species delenda*.

BOTHRIOCPHALUS HISTIOPHORUS Shipley

The writer would also like to call attention in this place to the fact that Shipley's (1901) *Bothriocephalus histiophorus* agrees in all essentials with *B. manubriformis*, which is almost to be expected since both are found in the same host genus.

The description and figure of the scolex is that of the latter species, altho the true nature of the bothria was not ascertained by Shipley on account of their almost closed condition, which was also seen in many specimens of *B. manubriformis* by the writer. Consequently it was described, erroneously, as ". . . provided with longitudinal slit-like depressions which hardly attain the dignity of suckers situated in the dorsal and ventral plane." The external features of the strobila are the same in both species, altho Shipley was describing a comparatively young specimen, as shown in his measurements of the scolex and in his figures showing the size of the uterus-sac. The description and figures of the genitalia agree in almost all details. It is quite apparent, however, that his Fig. V, diagrammatic it is true, is entirely misleading as to the proximal connections of the reproductive ducts, one of which, the ootype, he confused with the isthmus of the ovary. The ova in the latter were found by the writer to be 15μ in diameter in *B. manubriformis* as in *B. histiophorus*. His description of these central connections of the genital ducts is certainly not that of the genus Bothriocephalus; for in dealing with the isthmus of the ovary, which he called the ootype, he said that "Into this region opens the small shell-gland, and the ducts of the yolk glands. The shell-gland lies posteriorly to the ovary between the right and left halves of that organ and with the ducts of the yolk glands it opens into the ootype posteriorly." The measurements of the eggs and the description of the uterus agree with those of Linton's species, excepting that the opening of the uterus-sac ". . . does not seem to be provided with anything of the nature of a sphincter muscle. . ." Altho the material at hand did not permit of the sectioning of such young stages in the development of the uterus-sac, it would seem from the somewhat varying nature of its funnel-shaped ventral end, described above for *B. manubriformis*, that in more anterior proglottides it might be in such a condition as to be easily overlooked. The nature and arrangement of the vitelline glands, the vagina and its bulb or sphincter, the testes in number and position, and finally the cirrus-sac, all considered in connection with his Figs. I–IV, force the writer to the conclusion that, so far as can be determined in the absence of material for study, Shipley's *B. histiophorus* n. sp. is identical with *B. manubriformis* (Linton).

Concerning the probable disposal of ripe eggs in *B. histiophorus*, Shipley made a statement with which the writer can agree, since it seems to be the natural conclusion to arrive at after a study of the varying contents of the uterus-sac along the strobila, namely, "From what I have seen I think it prob-

able that eggs pass out from the tapeworm into the alimentary canal of the host and that in *B. histiophorus* the eggs pass freely out from each proglottis and do not wait until the posterior proglottides break off to make their escape from the parent."

In the following table a number of important measurements of *B. manubriformis*, *D. laciniatum* and *B. histiophorus* are given for the sake of comparison; all dimensions are given in millimeters:

	D. laciniatum	*B. histiophorus*	*B. manubriformis*
Maximum length of strobila	154		220
Maximum breadth of strobila	4		5
Breadth at posterior end	2		2
Length of scolex	2	1 8	1.5-3.5
Breadth of terminal disc	0 8	0 4	0 8-1 2
Breadth of scolex at middle	0.4		0.64
Breadth at posterior end	0 6		0 81
Breadth at constriction	0.25		0.21-0 44
Depth of terminal disc	0.5		0.89
Depth of scolex, middle	0.55		0.90-1.05
Depth at posterior end	0.35		0.63
Depth at constriction	0 25		0.58
Length of first segment	0.7		0.39
Breadth of same anteriorly	0 3		0 28-0.54
Breadth of same posteriorly	0 65		0 50-0.89
Length of median segments	0 3	0.3	
Breadth of median segments	0 3		
Length of posterior segments	1	0.16 ("ripe")	1.0
Breadth of same	1 5	0.5 ("ripe")	2.50
Length of cirrus-sac	0 4		0.50
Max. diameter of same	0 14		0 14
Length of vaginal sphincter	0.05		0.05
Diameter of same	0.07		0 07
Dimensions of eggs	52x35μ	45x35μ	58x34μ
Dimensions of calcareous bodies	17-24x8-14μ		18-26x11-15μ
Number of testes		50-70	60-70
Diameter of ova in ovarian isthmus		0.15	0.15

BOTHRIOCEPHALUS OCCIDENTALIS (Linton 1898)

[Figs. 28, 89]

1898	*Dibothrium occidentale*	Linton	1898 : 437
1899	*Bothriocephalus occidentalis*	Lühe	1899 : 43
1900	*Bothriocephalus occidentalis*	Ariola	1900 : 415

Specific diagnosis: With the characters of the genus. Large cestodes with maximum length at least 310mm. and breadth 5.5. Scolex small, elongate and somewhat rectangular, constricted posteriorly, 1.3mm. long by 0.46 wide. First segments somewhat funnel-shaped; middle, densely crowded, ten to twenty times broader than long; posterior narrower and longer, 2 by 0.8mm., in groups of three or four.

Cuticula 1.5μ in thickness. Calcareous bodies 18 by 13μ. Longitudinal muscles in bundles, outer series very scarce. Four chief excretory vessels, two much more prominent than the others.

Genital cloacae form a narrow zig-zag row, each very shallow, no velum, cloaca and hermaphroditic duct united. Vagina opens directly behind the cirrus or a little to one side.

Testes divided into two fields on each side by the nerve strand, 75 to 90 in number, 25, 85, and 115μ in average maximum length, breadth and depth. Coils of vas deferens loosely arranged, the duct 25μ in diameter, alternating irregularly from side to side opposite the uterus-sac. Cirrus long and cylindrical, 0.23 by 0.06mm., walls comparatively thin, most of the circular muscles being towards the inner end.

No vaginal sphincter nor bulb. Ovary solid, unbranched, 0.5 to 0.6mm. wide, 0.04 long and 0.13 to 0.18 deep. Oocapt 25μ in diameter. Vitelline follicles very numerous, the two lateral fields on each surface narrow, leaving a broad median strip free, 25, 60 and 115μ in length, breadth and depth, respectively. Vitelline reservoir 45μ in diameter. Uterine duct voluminous on both sides of the median line, crowding all other organs. Maximum width and length of uterus-sac, 0.65 and 0.25mm., respectively; not encroaching much on neighboring proglottides; ventral portion not especially modified. Uterus-openings alternate irregularly from side to side near the median line, far forward in the proglottides.

Eggs 72 to 76 by 38 to 41μ, dark brown, showing thru the walls of the distended uterus-sacs.

Habitat: Intestine and pyloric coeca of the "rock cod," Sebastodes sp.

Type specimen: No. 4740 in the collection of the United States Museum, collected by T. H. Bean and identified by Professor Edwin Linton.

Type locality: Whatcomb, Washington.

The material contained in lot No. 4740 of the collection of the United States Museum, upon which Linton based his species, was examined by the writer and confirmatory sections were made of mature segments; but it was all in such a very poor state of preservation that only a little can be added to the meagre descriptions already published.

Lühe (1899:43) stated under his diagnosis of the genus that "Von weniger gut bekannten Arten gehören auscheinend noch hierher *Bothriocephalus laciniatus* (Lint.) und *occidentalis* (Lint.)," while Ariola (1900:415) included it in his compendium of the known species.

Since no scolex and only very poorly preserved anterior parts of the strobila were found in the above mentioned lot, Linton's description is here given verbatim:

"The bottle contained two fragments and portion of pyloric coeca of fish. The fragments measured 190 and 310mm. in length, respectively. Another fragment with scolex was found in one of the pyloric coeca; this was 115mm. in length.

Head small, elongated truncate, and somewhat capitate, constricted near posterior end with prominent posterior margin; fossettes coincide with flat surface of body and extend posteriorly nearly to constriction; segments begin immediately behind head, somewhat funnel-shaped, soon becoming densely crowded and much broader, ten to twenty or more times as broad as long, decreasing in breadth and increasing in length again toward posterior end. Posterior segments in groups of three or four, namely, divisions between segments of contiguous groups more distinctly marked than between other adjacent segments.

Dimensions of head and segments: Length of head, 1.30mm.; breadth of head, apex, 0.46; middle, 0.46; base, 0.40; breadth of first segment, 0.42; length of first segment, 0.12; greatest breadth, 5.5; length of broadest segments, 0.25; breadth of posterior end, 2; length of posterior segments, 0.8. . . .

The sides of the head which correspond with the lateral margins of the body are medianly depressed toward anterior end."

Concerning the cuticula nothing more can be said than that in the anterior segments where it did not seem to be much eroded, it was found to be only about 1.5μ in thickness. The subcuticular cells are closely crowded together. They form a syncitioid layer, in which the comparatively large nuclei (8μ in diameter) stand out prominently, beginning about 35μ from the surface and extending centrally to the vitelline glands. As pointed out by Linton, "Calcareous bodies are present in the central core [medulla] and sparsely scattered elsewhere, but nowhere abundant. . . " The largest of them were found to be 18μ long by 13 wide, thus being within the limits of measurements of those of *B. manubriformis*.

In general the musculature is quite comparable to that of *B. manubriformis*. There is a stratum of frontal fibres on each surface of the layer of longitudinal fibres, but no third or outermost group in the anterior segments, doubtless owing to the fact that the posterior borders of the latter are not nearly so prominent. Both layers are related to the uteri and cirrus-sacs in the same way. The sagittal fibres are much less numerous especially anteriorly. While the main longitudinal muscles, arranged in quite the same manner and with the same thickness, namely, 145μ, render the cross-section of mature segments similar to that of *B. manubriformis* at first sight, the fibres of the external group

of this series are very scarce, confined to the anterior segments and very difficult to distinguish from the longitudinal cuticular fibres.

The nerve strands, each about 35μ in transverse diameter anteriorly and 85μ thick by 45μ wide in mature segments, are situated between the lateral and median quarters of the transverse diameter of the strobila. Unlike conditions in the foregoing species, they occupy either the whole of the dorsoventral diameter of the medulla or are situated strictly in the median frontal plane, depending on the degree of lateral contraction.

In the anterior segments two main longitudinal excretory vessels are located in the medulla between the nerve strands; while two others, much smaller and outside of the latter, are somewhat difficult to follow. In mature proglottides, however, all four vessels are fairly easily distinguished, especially in transections.

"The cirrus and vagina open by a common aperture on the middle of one of the flat surfaces of the body. . . . The vagina is behind the cirrus; in some cases directly behind it, in others a little to one side or other of the median line." This was found to be in the main true, altho on close examination it is to be seen that the common genital openings form a zig-zag row as in the foregoing species. The uterus-openings, described as opening "externally on the middle of the dorsal surface," likewise alternate irregularly from side to side. Furthermore, while the genital cloaca is situated at the middle of the very short proglottis, the opening of the uterus-sac is in the anterior portion of the segment, often being under the posterior border of the segment ahead. The cloaca itself is very shallow in this species, the openings of the cirrus and vagina being almost at the surface. There is no definite velum separating an inner ductus hermaphroditicus from an outer cloaca as in *B. manubriformis*.

In the sections made, the testes, divided into two fields on each side by the nerve strand, were much compressed anteroposteriorly with average maximum lengths, breadths and depths of 25, 85 and 115μ, respectively. On account of this crowded condition it was not found practicable to count their number directly in frontal sections, but it was calculated to be from 75 to 90. The vas deferens, averaging about 25μ in diameter, forms a number of loose, open coils extending thruout the whole dorsoventral diameter of the medulla on the side towards which the central end of the cirrus-sac is directed, and alternating irregularly from side to side as does the uterus-sac, but being constantly located on the opposite side of the median line from the latter. As it passes into the base of the cirrus pouch it has a diameter of only 3μ. In the proximal or central one-third of the sac it takes a few turns and then continues as a straight tube, somewhat larger (15μ) and usually filled with spermatozoa, the functional cirrus which is about 8μ in diameter. The cirrus-sac is elongate oval to cylindrical in shape, the slightly larger end is ventral, and has a maximum length and a diameter of 230 and 60μ, respectively. It is thus approximately only one-half as large as that of *B. manubriformis*; nor does it extend ventrally past the lower edge of the layer of main longitudinal muscles. Its wall, as shown in figure 89, is comparatively thin, as pointed out

by Linton, especially in the dorsal half, the inner layer of circular fibres being much more numerous ventrally. Thus there is left a comparatively large space around the ejaculatory duct to accommodate the retractor muslces and a small amount of parenchyma the nuclei of which are situated peripherally much as in *B. scorpii.* A character which distinguishes this species, however, from others of the genus is the presence of a loosely arranged bundle of muscle-fibres attached to the ventral end of the cirrus-sac and passing downwards between the coils of the uterine duct, beyond which they do not seem to have any definite attachment. Since the myoblasts and nuclei of these fibres are quite prominent, especially some distance from the cirrus-sac, the whole bundle has something of the appearance of an elongated gland. The protruded cirrus has a maximum length of 85μ with a diameter of 30μ. This everted condition of the cirrus, taken in conjunction with the nature of the genital cloaca described above, and the fact that there is no vaginal sphincter, points strongly to the cross-fertilization of at least different proglottides, rather than to self-fertilization. The former would, furthermore, seem possible between contiguous segments, since in many cases two consecutive cloacae were found close together and at the bottom of an apparently temporary depression of the dorsal surface.

The vagina has no sphincter, but begins somewhat broadly, as shown in Linton's figure 5, only to narrow down quickly to about 5μ half way along its course, which is almost straight ventrally. It expands slightly before joining the oviduct but does not form more than a temporarily functional seminal receptacle. The ovary, much compressed anteroposteriorly, is from 0.5 to 0.6mm. wide by only 40μ long at the isthmus, and from 0.13 to 0.18mm. deep. Its limbs are entire but much disturbed in their course laterally by the uterine ducts of contiguous proglottides. The oocapt has an average diameter of 25μ. Beyond it the oviduct enlarges, after constricting as usual, to about 25μ again where it is joined by the vagina. At the latter point there is a vestibule as in the last species. Just beyond this the oviduct is joined by the common vitelline duct which is enlarged near the junction to form the yolk reservoir or "central vitelline mass," about 45μ in diameter. The vitelline follicles are very numerous and closely arranged in the cortex in two lateral fields, leaving a broad median strip free of them on each surface of the strobila. Their maximum lengths, breadths and depths are 25, 60 and 115μ respectively; they have thus approximately the same bulk individually as those of *B. manubriformis.* They are continuous at the edges of the strobila and occupy the central one-half of the thickness of the cortical parenchyma, excepting in the median free strips. While the rather small shell-gland occupies a somewhat limited position dorsally at the level of the ventral end of the cirrus-pouch, the uterine duct takes so many coils, all of which are filled with eggs, in the median portion of the proglottis on both sides of the midline that most of the other structures are all but obliterated—at least at first sight. Both the uterine duct and the uterus-sac are arranged pretty much as in *B.manubriformis*; but the latter is only from 0.27 to 0.37mm. wide by about 0.15 long and about

0.35 deep in proglottides where the whole median portion is gorged with eggs. In the widest segments, however, they may attain a width of 0.65mm. by a length of 0.25 but at the same time not encroach so much on the neighboring segments as in the last species; for the length of the broadest segments, as given above, is 0.25mm. The lower portion of the sac is not modified into a funnel-shaped structure, while the actual opening is only about 15μ in diameter.

The measurements of the eggs are, according to Linton, 72 to 76μ in length by 38 to 41 in breadth. Such were found in the sections made, but no opercula such as shown in his figure 11; altho many similar appearances were considered to be only regular breaks in the shell.

From the above description it is to be seen that in many respects this species is very close to *B. manubriformis*. But in others it is sufficiently different to warrant the retention of Linton's designation, the more so in view of the fact that the host was taken from the Pacific coast, the bothriocephalid fauna of which has apparently not yet been touched.

CLESTOBOTHRIUM Lühe 1899

Bothriocephalus (part.)	Rudolphi	1819
Dibothrius (part.)	Rudolphi	1819
Bothriocephalus (part.)	Leuckart	1819
Bothriocephalus (part.)	Dujardin	1845
Dibothrium (part.)	Diesing	1850
Dibothrium (part.)	Molin	1858
Dibothrium (part.)	Diesing	1863
Bothriocephalus (part)	Carus	1885
Bothriocephalus (part.)	Ariola	1896
Clestobothrium	Lühe	1899
Bothriocephalus (part.)	Ariola	1900
Clestobothrium	Braun	1900

Scolex almost spherical, the free edges of the dorsoventrally situated bothria fused with each other in their whole extent in such a manner that only a small surficial opening near the apex leads into the interior of the spacious, hollow organ of attachment, flattened in the sagittal direction, by means of a short almost sagitally coursing canal which can be closed by a sphincter-like musculature. External segmentation complete. Vitelline follicles in the cortical parenchyma. Receptaculum seminis small. Beginning of the uterus a winding canal which leads into an extraordinarily spacious uterus-sac, distorting all other genital organs in ripe proglottides. Uterine opening about median as is the dorsal genital opening.

Type and only species: *C. crassiceps* (Rudolphi).

CLESTOBOTHRIUM CRASSICEPS (Rudolphi 1819)

[Figs. 29-31, 48, 49, 58, 74, 75, 90, 103, 108]

1819	*Bothriocephalus crassiceps*	Rudolphi	1819 : 139, 476
1819	*Bothriocephalus pilula*	Leuckart	1819 : 45
1845	*Bothriocephalus crassiceps*	Dujardin	1845 : 617
1850	*Dibothrium crassiceps*	Diesing	1850 : 587
1858	*Dibothrium crassiceps*	Molin	1858 : 134
1863	*Dibothrium crassiceps*	Diesing	1863 : 236
1885	*Bothriocephalus crassiceps*	Carus	1885 : 120
1896	*Bothriocephalus crassiceps*	Ariola	1896 : 280
1899	*Clestobothrium crassiceps*	Lühe	1899 : 44
1900	*Bothriocephalus crassiceps*	Ariola	1900 : 397
1900	*Clestobothrium crassiceps*	Braun	1900 : 1692
1901	*Dibothrium crassiceps*	Linton	1901 : 411, 451, 473
1909	*Dibothrium crassiceps*	Johnstone	1909 : 87

Specific diagnosis: With the characters of the genus. Medium sized cestodes, up to 92mm. in length, with a maximum breadth of 1.5mm. Anteriorly surface of body with closely arranged transverse furrows, posteriorly segmentation more distict, serrate. Scolex globose, 0.64 to 1.08mm. long, 0.52 to 0.90 broad, and 0.68 to 1.21 thick; divided by longitudinal marginal grooves into two dorsoventral hemispheres, the bothria. Latter large, prominent, oval, their apertures about one-third their length from the apex and connected by a saddle-shaped groove over the tip of the scolex, with prominent lips. No neck, segmentation beginning immediately behind the scolex. Young segments closely arranged, five to six times as broad as long; mature proglottides quadrate to twice as long as broad, frequently divided on one or both sides by spurious articulations usually behind the uterus-sacs.

Cuticula 2 to 5μ thick, subcuticula 20μ. Chalk-bodies absent. Musculature well developed, powerful sphincter around orifice of bothrium. Chief nerve strands ventral, 15 to 20μ in diameter. Usually four longitudinal excretory vessels.

Genital cloaca median, dorsal, three-fourths to one-half the length of the proglottis from its anterior end, usually just posterior to the spurious articulations; hermaphroditic duct within cloaca.

Testes in two lateral fields in the medulla; ellipsoidal in shape, 0.125mm. long by 0.04 in diameter, continuous from joint to joint, 40 to 50 in each proglottis. Vas deferens forms a wedge-shaped mass of coils ahead of cirrus-sac and alongside of the hinder end of the uterus-sac. Cirrus-sac elliptical to somewhat oval, 0.128 to 0.162mm. long by 0.087 to 0.116 wide and 0.098 to 0.116 deep, immediately behind the uterus-sac or lateral to its posterior end. Cirrus-sac and vas deferens together alternate irregularly from right to left opposite the hinder end of the uterus-sac.

Opening of vagina close behind that of cirrus. Receptaculum seminis present as a short diverticulum almost parallel to the oviduct at the point of union of the vagina with the latter, about 10μ in diameter. Ovary bilobed, the isthmus narrow and ventral, ova in same 18 by 10μ. Oocapt 20μ in dia-

meter. Vestibule at the point of union of the vagina with the oviduct. Vitelline duct expands into a reservoir 30μ in diameter. Vitelline follicles not in lateral fields, but continuous from joint to joint, 60 by 30 by 50μ in dimensions, about 700 in each proglottis. Uterus-sac elliptical in outline, directed anteroposteriorly in the anterior half of the proglottis, where in gravid segments it occupies almost the whole of the medullary region; 2.20 by 1.34mm. in dimensions; in quadrate segments irregularly alternating from side to side as are the uterine openings.

Eggs, 75 by 40μ.

Habitat: In the anterior portion of the intestine of the host.

HOST	LOCALITY	COLLECTOR	AUTHORITY
Gadus merluccius (Type host)	Naples	Rudolphi	Rudolphi 1819 : 139
Gadus merluccius		Leuckart	Leuckart 1819 : 45
Gadus merluccius	Patavia	Molin	Molin 1858 : 134
Gadus merluccius	Trieste	Stossich	Carus 1885 : 120
Gadus euxinus	Trieste	Stossich	Stossich 1899 : 1
Merlangus carbonarius	Nizza	Wagener	Wagener 1854 : 61
Merlangus sp.		Wagener	Wagener 1857 : 93
Merluccius bilinearis	Woods Hole	Linton	Linton 1901 : 473
Merluccius esculentus		Parona	Ariola 1896 : 265
Merluccius esculentus	Trieste	Stossich	Stossich 1898 : 115
Merluccius merluccius	Pisa	Wagener	Wagener 1854 : 68
Merluccius vulgaris	Ireland	Drummond	Thompson 1844 : 439
Merluccius vulgaris	Patavia	Molin	Molin 1861 : 235
Merluccius vulgaris	Pisa	Wagener	Diesing 1863 : 237
Merluccius vulgaris	Padova	Molin	Diesing 1863 : 237
Merluccius vulgaris	Genova	Parona	Ariola 1896 : 265
Merluccius vulgaris	Portaferrajo, Id. Elba	Damiani	Parona 1899 : 8
Merluccius vulgaris	Pisa	Parona	Parona 1899 : 8
Merluccius vulgaris	Gaeta	Ariola	Ariola 1900 : 397
Merluccius vulgaris	Augusta, Catania	Barbagallo and Drago	Barbagallo and Drago 1903 : 412
Pomatomus saltatrix	Woods Hole	Linton	Linton 1901 : 451
"A small hake"	Calf of Man, England	Johnstone	Johnstone 1909 : 87
Merluccius bilinearis	Passamaquoddy Bay, St. Andrews, N.B.	Cooper	Cooper (the present paper)
Merluccius bilinearis	Buzzards Bay, Mass.	Cooper	"
Merluccius bilinearis	Vineyard Sound, Mass.	Cooper	"
Merluccius bilinearis	Casco Bay, Me. South Harpswell	Cooper	"

In external appearance this species is characterized by the globose nature of the scolex and the serrate margins of the strobila, the former of which was the basis of Leuckart's (1819:45) specific name and which with the latter was emphasized and included in the diagnoses given by all the authors after Rudolphi (1819). But another important character which also assists in the ready recognition of the species is the presence of spurious articulations, which, however, are evidently not those mentioned collectively by Wagener (1854:69) as "articulatio spuria."

The scolex (Figs. 29-31) is divided by two longitudinal marginal grooves into two dorsoventral hemispheres, the bothria. The latter were considered by Rudolphi (1819:130, 477) and others to be marginal in position, but many years elapsed before this error was finally and definitely corrected by Lühe (1899:35). F. S. Leuckart (1819:45) rightly described and figured the scolex as "medio marginali sulcato, foveis lateralibus. . . ." and "Die Randfläche des Kopfes ist breiter als die Seitenfläche, die mittelfurche jener ziemlich tief, und bi det an jener Seite eine erhabene, in der Mitte hellere Wölbung." It seems that Molin (1881:235) fell into the error of considering the marginal or lateral grooves, separating the bothria, to be the bothria themselves, as indicated in his diagnosis: "Caput magnum subglobosum, utrinque sulco longitudinali laterali, apertura centrali bilabiata antica, bothriis ovalibus, subter minalibus, marginalibus, longis"; and in his "Osservazione 2" he said: "Quantunque la testa sia molta grossa ed opaca, ciò non per tanto potei distinguere il solco menzionato da Diesing [1850:587] il quale pero corrisponde ai lati e non ai margini del corpo, e sembra dividere la testa in due emisferi. Ognuno di questi porta una fossetta oblunga, ovale, che si estende dall' apice a due terzi della lunghezza del corpo, e sembra di quattro quadranti suddivisi da due solchi che s'incrocciano." It is evident from his figure 2, Taf. V, that the "fossetta oblunga" is the entrance to the bothrium, but he does not seem to have observed the actual opening. Matz (1892:103) expressed the opinion that the bothria of this species are dorsoventral in position, while Ariola (1896:280) evidently on the basis of former descriptions placed the species among those of the genus Bothriocephalus Rud. with "Botridi marginali." Stossich (1898: 115) also described the scolex as " . . . subglobosa, con botridii marginali, subterminali, ovato-allungati." Ariola (1900:398) finally corrected his own view of the external structure of the scolex by saying that "Un esame anche superficiale dimostra però che la posizione degli organi di fissazione non e equale fu ritenuta, perchè ciascun d'essi corrisponde ad una faccia larga dello strobila, o como si dice, sono dorsoventrali. I pretesi botridii marginali sono dati da un solco circulare, abbastanza profondo, che corre a guisa di un meridiano attorno allo scolice globoso, passando per l'apice, e dividuendolo come in due emisferi, uno destro a l'altro sinistro," thus evidently ignoring the fact that Lühe had already (1899:25) performed the service for students of the group, as he later pointed out with justifiable emphasis (Lühe, 1901:414).

The bothria in this species are sac-like structures, formed (phylogenetically) as indicated in the generic diagnosis, by the rolling together of their edges or

"walls" and the fusion of the latter for most of their extent "in such a manner that only a small lateral [dorsoventral] opening in the region of the apex leads into the anterior of the spacious, hollow organ of attachment." The size and shape of the opening itself varies considerably in preserved material. It may be so small (Fig. 29) as to be seen only on very close examination or in sections, or comparatively large (Fig. 49), depending on the stage of contraction or enlargement of the bothria when the individual is fixed or preserved. During life it may be seen to undergo such variations in size while the whole scolex isbeing elongated and retracted during the characteristic sucking movements. Rudolphi (1819:477) correctly described the bothria as ". . . oblonga profunda et magna in vivis; in mortuis bothrii ostium parvum anticum adesse videtur." In lateral view (Fig. 30) the bothria are seen to be more sharply oval or even conical in outline, as is consequently the whole scolex, owing to the fact that the dorsoventral diameter of the lumen of each is much greater in its posterior half than in its anterior half. It will also be noted more clearly from this aspect that the hinder borders of the bothria project a considerable distance beyond the true anterior end of the strobila. Thus the length of the scolex is not that of the bothrium, as many writers have evidently taken it to be, but as far as can be determined from external views, more nearly that of the marginal sulcus plus an extension of the same to the tip of the scolex, or, where the latter is retracted, to the anterior border of the labia. The breadth of the scolex is here taken for the sake of convenience to be that of the bothrium, since there is very little difference between the two in this regard. The two apertures of the bothria are united over the tip of the scolex by a saddle-shaped groove, the edges of which are somewhat swollen so as to form lip-like structures. This groove has been described and figured for *C. crassiceps* by Molin (1861:235, Fig. 2, Tab. V) and Ariola (1900:397, Fig. 17, Taf. VIII) and figured by Linton (1901a:Fig. 267, Pl. 24), but it does not appear either in the figures given by Wagener (1854:Fig. 75, Taf. 7; 1857:Fig. 6, Pl. II) or that by Johnstone (1909:87, Fig. 14). It is present in all of the writer's material even to the youngest, but in a few cases the tip of the groove, that is the extreme tip of the scolex, is so prominent as to more or less obliterate the lips (Fig. 49). It is also to be noted that the lateral grooves separating the bothria do not pass thru these lips. This is nicely indicated in Ariola's figure but erroneously described by him as "passando per l'apice," and as further figured but in the same relation by Johnstone. Wagener's figure 75 and Linton's figure 266 also give the erroneous impression that this groove passes right over the tip of the scolex. Molin (1861:235), while giving a somewhat confused description of the relations between the saddle-shaped structures—which he figures as including the apertures of the bothria more posteriorly—and the lateral grooves, says that he saw in the apex an aperture which not only ended blindly but which was bounded by two eminences, simulating lips. This may have been due to extreme contraction of the tip of the scolex between the lips of this groove. It will be recalled that Leuckart (1819:46) stated in this connection that "An dem Kopfende ist eine kleine Vertiefung in der Mitte; die von den

beiden sich hier vereinigenden Randfurchen herrührt, wodurch ihre Ränder etwas erhabener werden. Die Grübchen sind kaum von der Grösse eines Nadelknöpfchens und tief in Kopfe, so dass es fast scheinen könnte, als wären sie wahre oscula;" but his figure 26, very good in other respects, does not do justice to his description of these terminal structures. Compare also Lönnberg's (1893: 15-17) *B. neglectus*, the figure for the scolex of which looks very much like *B. crassiceps*.

There is no neck in this species, but segmentation begins immediately behind the scolex (Fig. 48) and is complete thruout the strobila. These characters were included by Lühe (1899:44) in the diagnosis of the genus: "Aussere Gliederung vollkommen, ein gegliederter Hals fehlt." As regards this quotation, it would appear that the "gegliederter" is either superfluous or a *lapsus calami* for "ungegliederter." The anterior border of the first segment, a greater part of which is obscured by the hinder edges of the bothria, is constantly somewhat narrower than the latter, but its posterior border is usually about the same width even in such contracted specimens (Fig. 29). Its outline is somewhat trapezoidal, while its length is slightly greater than that of the segment immediately following. The breadth of this first segment varies anteriorly from 0.40 to 0.92mm. and posteriorly from 0.65 to 1.16—Linton's measurements are 0.78 and 1.07, respectively. Following this the segments are closely set, five to six times as broad as long, while their somewhat thickened posterior borders protrude on either side (as well as dorsoventrally) so as to give the strobila a serrate appearance (Fig. 48). It is here that the formation of new proglottides takes place by the subdivision of preexisting segments. This serrate appearance is also present in the posterior part of the strobila, where the proglottides are quadrate to twice as long as broad.

Posteriorly each serration does not necessarily define the posterior border of a proglottis. This is due to the presence of spurious articulations, possibly included in Wagener's "articulatio spuria." These are furrows which arise laterally, where they do not stand out as distinctly, however, as the true posterior borders of the proglottides, but do not pass to the median line. They are not present in all of the posterior proglottides nor are they symmetrically arranged. In the following excerpt from his more complete diagnosis it is to be seen that Rudolphi (1819:477) did not refer to these structures:

"Articuli breves, margine posteriore incrassato utrinque exstante, quo corpus serratum fiat. Articuli ceterum inaequales, ut passim augustiores et longiores intercurrant." F. S. Leuckart said only, "Die ersten Glieder am Kopfe schmaler als die Übrigen, dann folgen fast gleichbreite, die letzte Hälfte der Glieder breiter als lang, mit deutlichen, weissen Ovarien," which statement refers to "der beschreibene nicht ganze Wurm . . . 1½" lang." Diesing (1863:236) described the strobila as " . . . ellipticum, articulis ad medium usque increscentibus, inde descrescentibus, marginalibus posticis utrinque prominentibus, articulo singulo plica transversali diviso . . . " The latter has reference obviously to Wagener's "articulo spuria." It is also seen that, as regards the shape of the strobila, he

(Diesing) was dealing with much contracted specimens, the length being cited as ranging from one and a half lines to two inches. Ariola (1900:397) gave the following description of the segments:

"Strobila anteriormente assai piu stretto dello scolice, a guisa di peduncolo; le primi proglottidi sono rettangulari, strette, ma rapidamente si allargano; raggiunta la massima dimensione, la conservano sino all ultimo tratto del corpo, dove nuovamente si restringono. Le proglottidi mature hanno angula posteriori appena visibili; le ultime presentano forma trapezoidale." And Johnstone (1909:89) stated, "The posterior proglottides are much broader (in the transverse axis of the strobila) than they are long (in the longitudinal axis of the strobila); and their anterior extremities are narrower than the posterior ones, so that the edge of the strobila appears to be serrated. Secondary segmentation of the proglottis often occurs."

In fine, Wagener, Diesing, and Johnstone are, to the writer's knowledge, the only writers who have referred to this spurious articulation or subdivision of the segments into false secondary segments—although Lühe (1902:629) repeated the statements of the first two authors. Furthermore, Wagener did not figure the adult strobila of the species to show the structures in question, but in the legend for his figure 79, Taf. 7 of *Dibothrium heteropleurum*,—now *Amphicotyle heteropleura* (Diesing)—says only that "Man sieht die articulo spurio, welche die echten Glieder, wie bei *Dibothrium crassiceps*, in der Mitte theilt"; and further, as regards the difference in structure of the sides of this species, "Der Schein entsteht durch die noch dichtere Zusammendrangung der Falten der wahren und falschen Glieder auf der concaven Seite." In the legend (p. 61) for his figure 6, the egg of *C. crassiceps*, he also said that "Jedes Glied hat in der Mitte eine Falte, die ihm das Ansehen giebt, als bestunde es aus zwei Gliedern." Thus, there is reason to believe that for this species no one (apart from Linton's Fig. 268) has as yet described nor figured what the writer here calls spurious articulations, but that these workers were referring to the secondary division of the segments of the anterior end of the strobila which proceeds in the manner described for *B. scorpii* et al., altho not so clearly (Figs. 48 and 58). This is borne out by the fact that the spurious articulations described here never reach the median line of the strobila, much less pass completely across it as do the true posterior borders of the proglottides (Fig. 74). In one moderately relaxed strobila the first segment showing spurious articulations appeared 11.7mm. from the tip of the scolex, while in another which was quite contracted, especially anteriorly, 4.8mm. In the former case the next two pairs of these structures—and all of these in question happened to be bilaterally symmetrically situated—appeared in the fourth and thirteenth segments following.

Posteriorly the uterus-sacs appear as a series of gradually enlarging, dark punctations, as described below, not so pronounced, however, as in *B. scorpii*. The measurements of the first proglottis showing eggs in the uterus-sac in a fairly relaxed strobila at hand were 0.50mm. in length by 0.92 in breadth, while for one farther back where the uterus-sac was 0.61 by 0.48

mm., they were 1.31mm. in length by 0.82 in width. These measurements are, however, of only relative value. Another strobila of the same age but contracted at the time of fixation might show the same regions more like those farther ahead and, thus, in alcoholic specimens, evidently younger.

The following table gives various external measurements of six specimens in alcohol for the purpose of comparison; all dimensions are in millimeters.

Length in mm.	87	92	43	Little more than scolex	29	72
Length of scolex (lateral view)	0.87	0.59	0.46	0.43	0.63	0.83
Length of bothrium	1.08	0.77	0.64	0.64	1.00	1.01
Breadth of same	0.75	0.57	0.52	0.53	0.67	0.90
Thickness of same	0.87	0.64	0.68	0.58	0.74	1.21
Breadth of segment I, anteriorly	Much contracted	0.40	0.37	.....	0.55	0.92
Breadth of same, posteriorly	Ditto	0.53	0.60	0.53	0.74	1.16
Thickness of same, posteriorly	0.37	0.38	0.24	0.27	0.52	.....
Maximum breadth in anterior part of strobila	1.01	0.82	1.06	.....	1.30	.....
Same in posterior part of strobila	1.11	1.04	1.16	....	1.48	1.38

The cuticula varies in thickness from 2 to 5μ, the most common measurement being about 2.6μ. Resting on a distinct basement membrane, well shown after the use of Mallory's stain, it is divided into two strata of equal thickness by a granular layer, the components of which seem to be related to the bases of the stout, somewhat club-shaped pseudocilia or "hairs" which constitute the outer moiety. While the inner stratum was found to be homogeneous with the stains used, the outer showed two intensities of color, an inner lighter and an outer darker. The former represents the narrowed central ends of the spindle- or club-shaped pseudocilia, while the latter is determined by the well-stained bodies of the cirri themselves. Linton (1901:473) said that "the cuticula is covered with minute spines," but Johnstone (1909:89) said, concerning these structures: "I can see nothing of this kind in the species before me." All over the scolex and in the form of a band on the posterior borders of the proglottides (Fig. 103) these cirri become modified into stouter spinelets from two or three times longer than elsewhere and everywhere directed posteriorly, quite like those described by the writer (1914a:85) for *Haplobothrium globuliforme*, but much longer relatively; thus indicating their function as accessory organs of attachment. The largest spinelets are in the middle of this band, those at the edges, that is in the anteroposterior direction, gradual-

ly merging in length into the pseudocilia of the cuticula of the neighborhood. Furthermore they are arranged in the same manner on the posterior borders of the spurious articulations and of all of the secondary segments situated in the anterior portion of the strobila. They were referred to by Wagener (1854: 5), Diesing (1863:236) as "articulo singulo . . . postice ciliis instructo," Cohn (1902:55) and by Lühe (1902:238, 247) who considered "dass es sich nicht um in die Cuticula eingesenkte Stacheln handelt, wie bei dem Stachelkleide so vieler Distomen, sondern nur am Fortsätze der Cuticula, durchaus analog denjenigen, welche Looss an der bereits oben citierten Stelle fur *Haematoloechus asper* abgebildet hat."

The subcuticula, about 20μ in thickness, consists of fairly elongated cells, the nuclei of which are situated at their central ends close to the vitelline follicles. Their boundaries are difficult to ascertain, the whole layer thus being more of the nature of a syncitium. For about one-third of their length immediately beneath the cuticula the cytoplasm becomes broken up into a number of more or less parallel processes which stand out in distinct contrast with the deeper inner ends of the cells, especially in transverse sections.

The parenchyma, everywhere encroached upon by the voluminous reproductive organs, is in the form of a comparatively open reticulum showing no features of special interest. It is naturally most abundant in the posterior flared ends of the proglottides. In small strobilas it is more compact in structure and contains relatively more nuclei. Distinct spaces, formerly occupied by calcareous bodies, such as are readily and distinctly seen in the parenchyma of *B. scorpii*, were found neither in the scolex nor in the strobila; nor were these structures noticed in living material.

The musculature is composed of the typical three sets of fibres, interfered with in the usual manner by the large reproductive organs and their external openings. The sagittal and frontal series are only moderately developed, while the longitudinal series is about 10μ in thickness and situated within the frontal series. Its fibres are arranged in bundles of irregular shape (in cross-section) and width but of this uniform thickness, excepting where they are naturally much flattened out dorsally and ventrally by the distended uterus-sac. They are also continuous from joint to joint. A very weakly developed series of outer longitudinal muscles is present, while the muscles of the posterior border of the proglottis (vide Lühe 1897a) are poorly developed, in fact even less so than in Bothriocephalus.

In the scolex the frontal fibres are better developed than the sagittal ones, and pass around the bothrium closer to its lumen than to its external surface, while the latter are mostly confined to the region between the bothria. The inner longitudinal muscles of the strobila pass forward into the scolex, dividing as they meet the lumina of the bothria to pass around them and attach themselves to the margins of the apertures. They are thus directed somewhat obliquely as shown in Johnstone's figure 18 and described as ". . . running irregularly, probably obliquely, round the walls of the bothrium. These no doubt function as constrictors of the latter." A few pass on forward to the

tip of the scolex to assist in activating that region. Between the bothria, however, they were found to be separated into dorsal and ventral layers as in the strobila, and not united into a single coronal band, as shown by Johnstone. The bothrial sphincter (Fig. 48) is a powerful bundle of fibres, about 0.07mm. in transverse section surrounding the aperture close to its cuticula. In transverse sections of the scolex it appears as a deeply staining mass on each side of the opening, also shown in Johnstone's figure 15. As it crosses the aperture anteriorly it becomes greatly attenuated. This with its comparatively great size at the sides and posteriorly accounts for the almost complete disappearance of the aperture in many adult, preserved scolices owing to the powerful contraction of this muscle from behind forward, thus diminishing the opening towards the tip of the scolex. From their arrangement it is to be seen that this sphincter, evidently a modified group of frontal fibres, and the longitudinal muscles in the scolex play a more important role in the movements of the bothria than do the other groups. On account of their oblique course the longitudinal fibres evidently act in diminishing the size of the lumen of the bothrium as well as do the circular frontal fibres of the latter.

The nervous system consists of two longitudinal strands which enlarge in tip of the scolex to form two somewhat elongated ganglia. The latter are united by only a few fibres, but they send out comparatively large nerves to the bothria. In the strobila the chief strands, each from 15 to 20μ in diameter, are situated ventrally in the medullary parenchyma, just within the longitudinal muscles and from one-fifth to one-quarter the width of the strobila from its lateral margins (Fig. 90). About halfway along the scolex the strands are about 80μ in diameter; but the ganglia are somewhat smaller and situated close together about 0.15mm. from the summit. In other words the chief strands enlarge and diverge gradually until the equatorial region of the scolex is reached and then diminish in size as they converge to form the ganglia. A pair of prominent nerves is sent forward on each side to supply the saddle-shaped groove described above. In young strobilas the nerve strands are situated midway between the dorsal and ventral surfaces, and not ventrally.

The excretory system consists of a pair of longitudinal vessels, situated ventrally, that is, in the same frontal plane as the chief nerve strands, each vessel being in the anterior end of the strobila about halfway between the nerve strand and the median row of reproductive rudiments. These vessels break up in a very irregular manner into extremely elongated loops, so that for considerable stretches four vessels will appear while again the branchings will be so numerous as to make it very difficult to decide, on looking at a transverse section, which are the main channels (Fig. 48). In other individuals four vessels appear, so that one is led to conclude that the pair just mentioned represent the latter, fused at times but separated again to form the loops. But whether these four vessels represent the typical four of other orders is a matter of conjecture. These main vessels may continue back into the ripe joints close alongside the uterus-sacs, but they usually break up into a very diffuse reticulum throughout the medullary parenchyma in the region where the openings

of the cirrus and vagina pierce the cuticula in development. Behind this region it was found impossible to trace the main vessels with satisfaction. The system usually passes into the scolex as two vessels, but soon breaks up into an elaborate net-work which ramifies between the bothria and throughout their walls. These branches are shown in Johnstone's figure 15. As regards the conditions of the excretory system in the extreme posterior end of the strobila, the material at hand permits of only negative conclusions. In the youngest strobilas, such as that shown in figure 49, the vessels converge posteriorly to open into a notch in the cuticula, there being no definite terminal vesicle such as is present in plerocercoids of the genus Proteocephalus, for instance. From this and the further fact that Wagener (1857:93) showed (Fig. 6, Pl. II) the main vessels in a very small strobila, which he examined while it was alive, passing separately to the outside, one is led to conclude that the vesicle, if ever present, must have been situated in the walls of an enveloping cyst and disappeared with the latter as in the Trypanorhyncha or the Cyclophyllidea. This seems to have been Wagener's idea of the situation when under his figure 65 (1854:68) he said: "Man sieht keinen pulsirenden Schlauch am spitzen Schwanzende. Es muss dies Thier auf ähnliche Weise entstanden sein, wie das in Fig. 74 dargestellte," and figure 74 is that of "Dibothrium (Belones ?)" from *Scyllium canicula* enclosed in a cyst in the walls of which "man sieht die Gefässe der Cestodenblase."

The earliest reference to the genitalia of *C. crassiceps* was by Rudolphi (1819:477) who said:

"Ova vel ovalia vel ovata, forsan secundun majorem maturitatis gradum. A B. punctato diversissimus, licet ovaria lateralia fuscescant, sed haec ipsa etiam in B. crassicipite quam in B. punctato majora sunt."

The structures called ovaria were evidently the uterus-sacs. F. S. Leuckart (1819:46) described the reproductive organs of his *B. pilula* as follows: ". . . die letzte Hälfte der Glieder breiter als lang, mit deutlichen, weissen ovarien. An den unteren Gliedern sieht man oberhalb jedes Eierstockes einen wasserhellen Punkt, wahrscheinlich Oeffnung fur das mannliches Zeugungsglied." From a comparison of this with his description and figure of posterior proglottides of *B. scorpii*, it is evident that he too was dealing with the uteri and their openings, respectively. He also referred to ". . . den schwarzen Punkten des Körpers, die Rudolphi fur Ovarien gehalten" of Redi's worm, which Rudolphi called (1810:67) *Bothriocephalus gadi merluccii* and placed in his "Species dubiae." Wagener (1854a:61) said that "Die Eier häufen sich in obersten Theile der Glieder an. Der Dotterstock verzweigt sich uber das ganze Glied und liegt overhalb der vescicules transparentes van Beneden. Die Geschlechtsöffnung ist in der Mitte und lateral." Diesing (1863:236) placed the "Aperturae genitalium laterales in linea mediana." Ariola (1896:265-266) gave the first comprehensive description of the reproductive organs in the following words:

"Tuttaria sul corpo si osservano macchie scure molto sporgenti, constituite della massa die uova. Tali rilievi non sono propriamente, nella linea mediana,

ma collocati a destra o a sinistra die essa formando in tal modo une striccia a zig-zag.

L'aperture genitale maschile sbocca sulla faccia dorsale, e sulle opposta si apre l'utero. In alcune proglottidi l'ovario e bilobo, la uova sono ellissoidali e mancano di operculo."

Lühe (1899:42-44) in defining the characters of the genus gave the general features of the genitalia, while Ariola (1900:397) enlarged his own 1896 description: "Ovario con numerose uova, talora bilobo; uova ellissoidali aventi nel diametro longitudinale 67μ e nel trasversale 32. . . ." Braun (1900) reviewed the literature on the genus and species up to date, and Volz (1900) discussed the reproductive organs of the species as compared with those of his *B. spiraliceps* and the position of the openings in connection with brief remarks on the phylogeny of the genus *Bothriocephalus* s. lat. As regards his own specimens Linton (1901:473) said that "Posterior segments show rudiments only of the reproductive organs, but no indication of external genital openings." And later Johnstone (p. 89) remarked that "the genital openings are in the middle line of the proglottides but near the anterior borders of the latter," referring evidently, as will be seen later, to the uterine openings only.

The rudiments of the reproductive organs appear about three millimetres from the tip of the scolex as aggregations of nuclei that can just be discerned in toto mounts (Fig. 48). About three millimetres farther posteriorly in moderately contracted older strobilas (such as would be obtained if no special care were taken during the fixation of the material) the cirrus and vagina are seen to be just piercing the dorsal surface. Before this region is reached, however, the common rudiment, at first circular and then elongated oval in outline, differentiates into a more anterior portion, the rudiment of the whole uterus, a more posterior less elongated part, the beginnings of the cirrus-pouch and vagina, and a third, connecting the other two near the hinder edge of the proglottis, the nuclear aggregation that will develop into the ovaries and the organs of the interovarial space (Fig. 74). As mentioned in the specific diagnosis, the first two of these rudiments alternate irregularly from side to side as do the corresponding adult structures. At the same time the testes and vitelline glands are developing in the medullary and cortical portions of the parenchyma, respectively.

A distinct genital sinus or cloaca, the opening of which is usually almost circular in outline, is present (Fig. 75). It varies from 0.05 to 0.09mm. in diameter and is situated, as above noted, nearly in the median line, dorsally, and from three-fourths to one-half the length of the proglottis from its anterior border, usually just posterior to the spurious articulations when they are present. At the bottom of this sinus there is a secondary cloaca ("Geschlechstasche" or "Ductus hermaphroditious"), also circular in outline, from 15 to 25μ in diameter, and into it open the cirrus and vagina quite close together, the latter immediately behind the former. This secondary sinus is best seen in sagittal sections (Fig. 103). The genital pore (the opening of the main sinus) is elevated slightly above the general dorsal surface of the proglottis,

thus appearing as a low cone or crater. No sphincters control the openings of either of these sinuses but the cuticula of the floor of the larger or outer is modified to form coarse, low, rounded and closely set papillae which are evidently of special importance during copulation. These papillae would evidently serve to temporarily fasten the structure into the primary sinus of another proglottis, when it is possibly everted with the cirrus. Copulation was not observed in this species during life, nor were any cases of protruded cirrus met with in the material at hand.

All of the proximal portions of the reproductive organs, excepting the vitelline follicles, are located in the medullary parenchyma, although the much distended uterus-sac, originally in the latter, extends almost to the cuticula on both the dorsal and ventral surfaces. Figure 75 shows their arrangement in toto.

The testes are closely arranged in the medullary parenchyma in two lateral fields, each bounded laterally by the junctions of the dorsal and ventral layers of longitudinal muscles and medially by the other reproductive organs (excepting the vitelline glands) which occupy in the quadrate proglottides about the middle one-third of the transverse diameter of the strobila and are contiguous from joint to joint. In the quite mature elongated proglottides the testes are ellipsoidal in shape, averaging 0.125mm. in length by 0.040 in diameter, the cross-section being usually about circular in outline. In younger joints and in all those of much contracted strobilas the testes are nearly spherical in shape, measuring about 60μ in diameter, or often slightly longer than broad. They are arranged in a single layer in the medulla, the whole dorsoventral diameter of which they occupy, and are continuous from proglottis to proglottis. From 2 to 4 appear in each lateral field in transverse sections, from 5 to 7 are seen in sagittal sections between the posterior borders of consecutive proglottides, while, so far as could be determined from frontal series directly, the number is from 20 to 25. Thus each proglottis contains from 40 to 50 testes.

The vas deferens forms a wedge-shaped mass of closely arranged coils, extending forward immediately ahead of the cirrus-pouch and alongside the uterus-sac for about two-thirds of its length (Fig. 75). In proglottides in which the latter is yet comparatively small the vas deferens may pass forward as far as its anterior end. In either case it forms with the cirrus-pouch a mass which alternates from right to left with the uterus-sac. When distended with sperms the duct averages about 30μ in diameter; but just before it enters the cirrus-sac anterodorsally it narrows down to 5μ. Immediately within the wall of the latter it often enlarges again to form a thin-walled functional vesicula seminalis, or perhaps more correctly ductus ejaculatorius, from 13 to 23μ in diameter. After one or two short turns it diminishes again to about 8μ and then passes on as the cirrus proper. While the proximal portions of the duct do not pass in any definite direction, the latter is situated for most of its length in the longitudinal axis of the pouch. It is about 0.10mm. in length and about 20 to 25μ in diameter at its middle. It is lined with a cuticula, 10μ thick, which is cleft but not armed with bristles of any kind.

The cirrus-sac (Fig. 103), situated immediately behind the uterus sac or lateral to its posterior end, is elliptical to slightly oval in outline, and measures 0.128 to 0.162mm. long, 0.087 to 0.116 wide and 0.098 to 0.116 deep. The longitudinal axis is directed anterodorsally from the genital sinus and to the right or left, according as it alternates with the uterus-sac. The proximal one-third of the contents of the pouch consists of loose parenchymatous tissue with a few muscle fibres surrounding the ductus ejaculatorius, while the distal two-thirds, that part which accommodates the cirrus proper, is supplied mostly with muscles which actuate the latter. Large fibres proceed somewhat obliquely from the wall towards the proximal pole of the sac to become broken up or frayed before they are attached to the cirrus tangentially, so as to give the appearance in frontal sections of the latter being surrounded by a comparatively heavy layer of fine lightly staining circular fibres. A few of the fibres closest to the cuticula of the cirrus were considered to be true circular fibres; but no longitudinal fibres were seen. The wall of the cirrus-sac is from 2 to 3μ thick and is made up of very fine closely matted fibres, the direction of which could not be determined with satisfaction. The sac lies freely in the parenchyma of the region and is not connected by any special muscles to the dorsal or ventral body-walls; nor are the body muscles attached to it as in some cestodes. The layers of the latter are simply pierced and the fibres turned aside in evidently a passive manner.

The opening of the vagina is close behind that of the cirrus at the bottom of the secondary genital sinus, or as it has been called by Fuhrmann, "ductus hermaphroditicus" (Fig. 103). From this point the duct courses ventroposteriorly in the mid-line and then parallel to the dorsal surface of the proglottis until it reaches the ovarian isthmus, above which it makes a few turns and quickly diminishes from 20μ in diameter half way along its course to 10μ. It then dips farther down into the genital space, often enlarging slightly as it does, and soon joins the oviduct at an enlargement of the latter situated a short distance behind the oocapt. Throughout its length it is lined with a ragged or pseudociliated cuticula and surrounded by radially arranged nuclei connected with the cuticula by cytoplasmic strands like those described by the writer for *H. globuliforme* (1914a:105) and considered to be possibly extruded nuclei of the original epithelium as well as the myoblastic nuclei of circular fibres, a layer of which surrounds the duct. There is no vaginal sphincter.

In his generic diagnosis Lühe states that the receptaculum seminis is small and in his description of the family Ptychobothriidae (1902:327) says that when present it is "in Gestalt eines kleinen Blindsäckchens ausgebildet, welches parallel neben dem Endabschnitte des Oviduktes liegt and mit der Vagina unmittelbar vor deren Vereinigung mit dem Ovidukt in Vergindung steht." On the contrary it was found to be a comparatively large structure but very difficult to orient in sections made in any direction. It is in the form of a thin-walled sac about 60 by 20μ, wrapped somewhat spirally around the dorsal wall of the above-mentioned enlargement of the oviduct and opening by an

aperture equal to its whole diameter into the vagina just at its juncture with this vestibule. But since the vagina constantly constricts a second time to a diameter of about 8μ before entering the latter, one gets the impression of the receptaculum seminis being a diverticulum of the oviduct rather than of the vagina. Figure 108 of four consecutive sections of a transverse series, showing the union of these ducts, will give a better idea, perhaps, of the nature of the seminal receptacle.

In mature proglottides the ovary (Fig. 90) is a bilobed structure situated in the median line, close to the posterior border of the proglottis and immediately ahead of the uterus-sac of the proglottis following, where the latter is much distended with eggs (Fig. 75). In toto mounts the lobes seem to be quite separate from each other, but in sections the isthmus is easily made out. It occupies the ventral half of the medulla while the wings or lobes extend completely across the space between the layers of longitudinal body muscles. The lobes are about 0.27mm. long by 0.13 wide, while the isthmus is 0.06 to 0.08mm. in anteroposterior diameter. These proportions are, however, much different in much contracted strobilas or in proglottides in which the uterus-sac is distended with eggs. In both instances the ovary is very much flattened anteroposteriorly and, in the latter case, all but obliterated, as shown in Lühe's figure 8 (1902:326). The ova from that portion of the isthmus where they are ready to be passed on by the oocapt, are elliptical to oval in outline in sections and measure on the average 18 by 10μ, their nuclei being about 9μ in diameter.

The oocapt, situated in the median line at the posterior border of the ovarian isthmus, somewhat dorsally, is a spherical to ovoid muscular organ about 20μ in diameter (Fig. 103). Immediately behind it the oviduct constricts to a diameter of only 7 to 10μ and then passes on posteriorly and ventrally either to the right or to the left, gradually enlarging until the above-mentioned vestibule is reached, when the diameter is 25 to 30μ. The latter enlargement is less of the nature of a direct continuation of the oviduct than a more or less separate thin-walled structure—the walls of the oviduct up to this point being comparatively thick (Fig. 108)—into which the oviduct opens by a slightly elongated aperture. While the wall of the first portion of the oviduct consists of more or less cubical ciliated cells with somewhat indefinite boundaries—ordinarily they stain very densely—that of the vestibule shows only a few scattered nuclei protruding into the lumen. The oviduct continues posterolaterally and ventrally from one corner of the vestibule (that with which the vagina is usually connected) as a tube quickly diminishing from 15 to 10μ in diameter and lined with a ciliated epithelium with prominent nuclei but no distinct cell-boundaries. Close to the anterior wall of the uterus-sac of the succeeding proglottis it turns upward sharply and at about the middle of the dorsoventral diameter of the medulla takes on the vitelline duct. It then skirts the uterus-sac, just mentioned, as it passes to the opposite side of the generative space and slightly forward, to soon become surrounded by the shell-gland.

The vitelline duct at its union with the oviduct has a diameter of 8μ; but just beyond this, in the direction of the follicles, it soon enlarges to form a somewhat irregular vitelline reservoir which when filled with yolk may attain a diameter of 30μ. Its general course is towards the opposite side of the generative space almost parallel to either surface of the body; but beyond this it could not be traced with satisfaction.

The vitelline follicles fill up almost the whole of the cortical parenchyma from the layer of longitudinal body muscles to the nuclei of the subcuticula, the thickness of the stratum averaging 0.05mm. (Fig. 90). They form a continuous layer around the margins of the proglottides (in transverse sections) and also from proglottis to proglottis, as mentioned above, even extending well into the posterior borders. They are not arranged in lateral fields, but are interrupted only where the uterus sac and genital sinus pierce the body-wall, or in the former case greatly press against the latter. The individual follicles attain a size of 60μ and are very closely crowded together. The number in cross-sections of the proglottis averages 55 and in sagittal sections 13, thus making the average total number for each proglottis 715.

The shell-gland is situated in the dorsal portion of the genital space, that part of the oviduct showing the connections being almost horizontal in position and about 18μ in diameter, that is, a little larger than the oviduct behind that region. The individual cells of the gland are much attenuated, closely arranged and have their nuclei situated in their slightly enlarged distal ends. Their connections with the oviduct give the wall of the latter a honeycombed appearance when it is seen in longitudinal section.

Beyond this region the oviduct gradually enlarges as it passes above the ovarian isthmus to become the uterine tube, the coils of which are accommodated opposite the cirrus pouch just behind the uterus-sac. As it proceeds its wall gets thinner and the nuclei protrude more and more into the lumen until many of them are evidently lost. It is noteworthy that the uterine tube in many cases as well as the uterus-sac, especially in younger proglottides, alternates irregularly from right to left according as the cirrus and vas deferens do. These three structures are, in fact, fitted very nicely into the space between the uterus-sac ahead and the ovarian isthmus behind.

The uterus-sac is elliptical in outline, has its longitudinal axis directed anteroposteriorly, and is situated in the anterior half of the proglottis. In very mature segments it occupies almost the whole of the medullary region, or to be more precise, the middle three-fifths of the diameter of the proglottis, its anterior end extending forward close to the ovary of the proglottis immediately ahead (Fig. 75). Lühe (1902a:326) figured the uterus as, to use his own words, " . . . in der Regel eine geräumige Uterushöhle bildend, welche die übrigen Genitalorgane, ohne dass freilich deren Rückbildung eintritt, buchstäblich an die Wand drängen kann, indem die ganze Proglottis in reifen Proglottiden vielfach als ein einziger sackförmiger Eibehalter mit verhältnissmässig sehr dünnen Wandungen erscheint." But such a degree of restriction of the other genitalia was seen by the writer only in a few of the ripe proglottides of strobilas

much contracted longitudinally. There the largest uterus-sac measured 0.8mm. wide by 0.67 long, while the width of the proglottis in question was, at the posterior borders of the spurious articulations, 1.57mm. In fairly relaxed strobilas it increases in dimensions from 0.18 by 0.14mm., where the first eggs appear in the lumen, to 0.87mm. long by 0.48mm. wide, where the proglottis is 0.80mm. wide at its middle, in the latter case, of course, pressing against the dorsal and ventral walls even as far as the cuticula. From a comparison of these measurements, and the further fact that in the case of the former much contracted strobilas there often appears, behind the region showing the nearly obliterated genitalia, a more relaxed one in which the relations of the uterus-sac to the other organs is quite as in the competely relaxed strobilas, one is inclined to conclude that the characters of the family above quoted apply to this species only in the case of proglottides much contracted longitudinally. In the quadrate proglottides the smaller, that is, younger sacs alternate irregularly from right to left, as do the uterine openings, and according as the cirrus pouch and the vas deferens in particular (on account of its above-mentioned position) occupy the opposite sides of the proglottis. Externally, in alcoholic specimens, the uteri appear as a gradually enlarging series of brown punctations caused by the contained eggs showing through the thinned body wall, as pointed out originally by Rudolphi and other writers.

The wall of the uterus consists of a thin membrane on the inside of which a very few scattered and somewhat flattened nuclei indicate its original epithelial nature. In young proglottides, where no eggs are to be seen in the small uterine cavities, the wall is composed of an epithelium about 8μ thick, showing prominent nuclei but no distinct cell-boundaries. Furthermore in such early stages the lumina of the uterine ducts, developing in the manner described by Young (1913) and Shaefer (1913), are not completely formed nor in connection with the cavities of the sacs, but the uterine apertures are prominent. In the first two or three sections of a 10μ frontal series, taken from the ventral surface, they appear as distinct somewhat elliptical apertures about 26μ in transverse diameter, but in the third or fourth section are closed, only to reopen as the cavity of the uterus-sac, thus showing that the membrane closing the aperture is only about 10μ in thickness. And this closed condition is maintained until the uterus-sac attains the above-mentioned maximum size and becomes greatly distended with eggs. Then the functional opening is established by the rupture of the membrane which has meanwhile reached a length of 0.046 to 0.058mm. by a width of 0.034 to 0.046, its elliptical outline thus having been retained. The opening does not become as regular in outline, however, as the membrane, for the latter remains around the rim as ragged processes, which render the determination of the exact location of the aperture in toto mounts a matter of no little difficulty. The uterus opening is surrounded by a series of radiating cells like those of the opening of *B. scorpii* described above.

The fresh eggs examined in saline solution are elliptical to ovoid in shape, 75 by 40μ in dimensions and provided with a thin, very light brown shell hav-

ing no operculum. The color is so faint that it can be seen to advantage only when the eggs are in masses or in the uterus-sac. Ariola (1900:397) gave the measurements of the eggs of the European species as 67 by 32μ. The largest examined were immature, the contents consisting of large spherical cells only, like those shown by Wagener (1854a) in his figure 6, Taf. I. When the worms are still attached to the wall of the intestine of the host between the mucous folds, they often discharge many of their eggs from most of the posterior proglottides when their scolices are irritated with a blunt needle in order to make them loosen their comparatively firm hold.

Forty-four specimens of *Merluccius bilinearis* were examined at Woods Hole and at Harpswell, but no definite idea of a possible intermediate host was obtained. It was noticed, however, that when the intestine of the fish contained much grey chyle, presumably the result of the digestion of small herring—definitely ascertained at South Harpswell to be such in a few cases—and of *Pomolobus aestivalis* (Mitchill), the blueback—no tape-worms of this species were present; but where amphipoda were found in the stomach or the remains of such in the intestine the worm was plentiful. Furthermore, where nothing was found in either stomach or intestines, other than yellowish chyle in the latter—as in most fish examined—indicating amphipods and other small crustaceans as food rather than small herring, the worm was also common. All stages from the youngest strobilas, such as that shown in figure 49, to the oldest were found, but none nor any plerocercoids were met with in the course of the thoro dissection of the available stomach contents of the hosts, both fish and crustaceans. In a number of cases, nevertheless, only very young strobilas were found in the intestine of the host, thus pointing to possible sudden infections at different times. Wagener, who figured the youngest strobila that has yet been recorded, in fact nothing much more than the scolex, said nothing more concerning the life history than that, on account of the excretory vessels opening separately to the exterior in this very young specimen, there might possibly have been a vesicular appendage to the larva in the nature of an enveloping cyst comparable to that described and figure for "Dibothrium (Belones?)" from *Scyllium canicula*, concerning which he said (l.c., p. 45): "Vergleicht man diese Form vom Cysticercus mit den vorigen [*Cysticercus fascicolaris* Rud.], so ergiebt sich, das der Unterschied nur in dem Aufhängebeutel sich findet, der Kopf und Blase verbindet."

A detailed description of the species is here given, not only because it is evidently the only one belonging to the genus, but because descriptive details are so lacking from the European literature that the determination of the species is attended with considerable uncertainty. The writer, however, considers that, on the basis of the published accounts and reports of the species, but in the absence of European material for comparison, the form occurring on this side of the Atlantic Ocean must be looked upon as identical with the *C. crassiceps* of Europe.

The material studied consisted of No. 204, 259, 261, 262, 269, and 282 in the writer's collection from the intestine of *Merluccius bilinearis* as above listed.

AMPHICOTYLINAE Lühe 1902

Scolex with two typical, usually not very deep bothria, which in some forms develop posterior, sucker-like portions. In an isolated case a pseudoscolex is substituted for the scolex. External segmentation insignificant, at times disappearing thru accessory wrinkling or folding of the surfaces of the proglottides. Opening of cirrus and vaginal marginal, irregularly alternating, with more or less strongly pronounced tendency to unilaterality. Uterus-opening median; uterus-sac always well developed. Coiling of vas deferens strongly expressed.

Occurrence: In fishes.

Type genus: Amphicotyle (Diesing 1864) Ariola 1900, e.p. Lühe 1902.

ABOTHRIUM van Beneden 1871, char. emend. Lühe 1899

Taenia (part.)	Auctorum	
Rhytis (part.)	Zeder	1803
Bothriocephalus (part.)	Rudolphi	1809
Bothriocephalus (part.)	Rudolphi	1819
Bothriocephalus (part.)	Leuckart	1819
Dibothrium (part.)	Diesing	1850
Bothriocephalus (part.)	Baird	1853
Dibothrium (part.)	Diesing	1863
Bothriocephalus (part.)	Olsson	1867
Abothrium	Beneden	1871
Abothrium	Moniez	1881
Dibothrium (part.)	Linton	1890
Abothrium	Lönnberg	1891
Bothriocephalus (part.)	Matz	1892
Bothriotaenia (part.)	Ariola	1896
Bothriotaenia (part.)	Riggenbach	1896
Abothrium	Lühe	1899
Bothriotaenia (part.)	Ariola	1900
Abothrium	Lühe	1900
Abothrium	Lühe	1910

Scolex not exceptionally elongated, with two powerful but not especially deep bothria. Segmentation in older portions of the strobila usually insignificant on account of superficial wrinkling of the individual proglottides; ripe proglottides essentially broader than long. Longitudinal nerves near the lateral borders, dorsal to the cirrus-sac and vagina. Testes exclusively between the nerve strands. Vitelline follicles of very irregular shape, in two broad lateral fields, in part at least between the bundles of the longitudinal muscles, the follicles of individual proglottides not especially separated from one another. Ovary scarcely lobed, more or less bean- or kidney-shaped. Shell-gland dorsal to the ovary. Uterus-sac in ripe proglottides occupying the whole of the medullary parenchyma. The openings of the uteri correspond to a more or less prominent median longitudinal furrow of the chain of proglottides.

Type species: *A. rugosum* (Batsch).

ABOTHRIUM RUGOSUM (Batsch 1786)

[Figs. 32–36, 63, 76, 91, 109]

1773	*Taenia decimpollicaris*	Strussenfelt	1773 : 27
1781	*Taenia tetragonoceps* (part.)	Pallas	1781 : 88
1782	"Der runzlichter Fischbandwurm"	Goeze	1782 : 410
1786	*Taenia rugosa*	Batsch	1786 : 208
1788	*Taenia tetragonoceps* (part.)	Schrank	1788 : 46
1790	*Taenia rugosa*	Gmelin	1790 : 3078
1802	*Taenia rugosa*	Rudolphi	1802 : 107
1803	*Rhytis conoceps*	Zeder	1803 : 292
1810	*Bothriocephalus rugosus*	Rudolphi	1810 : 42
1816	*Bothrioceophalus rugosus*	Lamarck	1816 : 168
1819	*Bothriocephalus rugosus*	Rudolphi	1819 : 137
1819	*Bothriocephalus rugosus*	Leuckart	1819 : 57
1845	*Bothriocephalus rugosus*	Dujardin	1845 : 618
1850	*Dibothrium rugosum*	Diesing	1850 : 591
1853	*Bothriocephalus rugosus*	Baird	1853 : 88
1863	*Dibothrium rugosum*	Diesing	1863 : 239
1867	*Bothriocephalus rugosus*	Olsson	1867 : 53
1871	*Abothrium gadi*	Van Beneden	1871 : 56
1881	*Abothrium gadi*	Moniez	1881 : 167
1889	*Bothriocephalus rugosus*	Linstow	1889 : 242
1889	*Bothriocephalus rugosus*	Monticelli	1889 : 68
1890	*Dibothrium rugosum*	Linton	1890 : 750
1890	*Abothrium rugosum*	Lönnberg	1890 : 22
1891	*Abothrium rugosum*	Lönnberg	1891 : 75
1892	*Bothriocephalus rugosus*	Matz	1892 : 113
1894	*Bothriotaenia rugosa*	Blanchard	1894 : 701
1896	*Bothriotaenia rugosa*	Ariola	1896 : 280
1896	*Bothriotaenia rugosa*	Riggenbach	1896 : 223, 228
1898	*Bothriotaenia rugosa*	Muehling	1898 : 35
1899	*Abothrium rugosum*	Lühe	1899 : 39
1900	*Bothriotaenia rugosa*	Ariola	1900 : 432
1900	*Abothrium rugosum*	Lühe	1900a : 101
1901	*Dibothrium rugosum*	Linton	1901 : 412, 476
1903	*Bothriotaenia rugosa*	Schneider	1903 : 7
1910	*Abothrium rugosum*	Lühe	1910 : 26

Specific diagnosis: With the characters of the genus. Large cestodes with maximum length, breadth and thickness of 1000, 7 and 2mm., respectively. Scolex present only in very young strobilas, when conical and provided with very weak bothria, changing with age to a pseudoscolex of various shapes, usually imbedded in pyloric cecum of host. Proglottides at first broad and very short, obscured by irregular transverse and longitudinal rugae, then gradually lengthening with age until finally quadrate or longer than broad.

Cuticula 5μ thick, subcuticula 0.14mm. Small calcareous bodies, 20μ in length. Longitudinal muscles in bundles, transverse forming septa between proglottides. Nerve strands 45μ in diameter. Two chief excretory vessels anteriorly, passing into 30 to 35 posteriorly.

Genital cloaca irregularly alternating, between first and second thirds of edges of proglottides. Vagina opens immediately behind the cirrus and slightly ventral; no hermaphroditic duct.

Testes discontinuous from proglottis to proglottis, ellipsoidal, flattened anteroposteriorly, 40 by 90 by 85μ, and 45 to 60 in number. Vas deferens lateral to uterus-sac with few coils before entering the cirrus-sac, 350 by 70 to 80μ. Cirrus-sac ovoid with narrow end outward, 174 to 277μ long by 92 to 102μ in diameter. Cirrus straight in outer half of sac, proximally coiled or dilated.

Ovary large, entire, kidney-shaped (isthmus as thick as the wings), 0.6mm. wide, occupying the posterior half of the median portion of early mature segments. Ova conspicuous, nuclei large, 10 to 13μ in diameter. Oocapt 34μ in diameter. Beginning of oviduct S-shaped. Right and left vitelline ducts join ventrally; common duct acts as reservoir. Vitelline follicles entirely within longitudinal muscles, discontinuous, intermingling laterally with the testes, irregular in shape and size, largest 30, 90 and 70μ in length, width and thickness, respectively. Shell-gland compact. Uterine duct with only a few coils close to the median line; uterus-sac very wide and short, or irregularly circular or quadrate surficially, often lobed, 0.75 to 1.6mm. in transverse diameter, constantly rounded laterally; openings in median zig-zag row.

Eggs, 80 to 98μ long by 75 to 92μ wide, shell quite transparent.

Habitat: Intestine of the host with pseudoscolex imbedded in a pyloric coecum.

HOST	LOCALITY	COLLECTOR	AUTHORITY	
Gadus mustela	....	Borke	Goeze	1782 : 410
Gadus mustela	.....	Wagler	Goeze	1782 : 411
Gadus aeglifinus	Warberg	Olsson	Olsson	1867 : 54
Gadus aeglifinus	Bergen	Lönnberg	Lönnberg	1890 : 22
Gadus aeglifinus	Grafverna and Näset	Olsson	Olsson	1893 : 17
Gadus aeglifinus	Arctic Ocean	Zool. Mus. d. K. Akad. Wiss., Petrograd	Linstow	1901 : 281
Gadus aeglifinus	England	Nicoll	Nicoll	1907 : 71
Gadus callarias	Woods Hole, Mass.	V. N. Edwards	Linton	1898 : 431
Gadus callarias	Arctic Ocean	Zool. Mus. d. K. Akad. Wiss., Petrograd	Linstow	1901 : 281
Gadus callarias	Murman-Küste	Zool. Mus. d. K. Akad. Wiss., Petrograd	Linstow	1903 : 19
Gadus callarias	Nokujev Id., Arctic	Zool. Mus. d. K. Akad. Wiss., Petrograd (Baer)	Linstow	1903 : 19
Gadus lota	Greiphswald	Rudolphi	Rudolphi	1810 : 43
Gadus merluccius	Rennes, France	Dujardin	Dujardin	1845 : 617
Gadus morrhua	Warberg	Olsson	Olsson	1867 : 54
Gadus morrhua	Grand Banks, Newfoundland	Lee	Linton	1890 : 750

HOST	LOCALITY	COLLECTOR	AUTHORITY
Gadus morrhua	Bergen	Lönnberg	Lönnberg 1890 : 23
Gadus pollachius	Rennes	Dujardin	Dujardin 1845 : 617
Gadus pollachius	Warberg	Olsson	Olsson 1867 : 54
Gadus pollachius	Bergen	Lönnberg	Lönnberg 1890 : 22
Gadus pollachius	Grafverna & Näset, Sweden	Olsson	Olsson 1893 : 17
Gadus pollachius	Millport, Scotland	Nicoll	Nicoll 1910 : 355
Lota vulgaris	.....	Siebold	Baird 1853 : 89
Lota vulgaris	Memel and Rossitten	Muehling	Muehling 1898 : 35
Lota vulgaris	Tvärminne Id., Finland	Schneider	Schneider 1903b : 8
Morrhua aeglifinus	England	Cobbold	Cobbold 1858 : 158
Morrhua vulgaris	England	Cobbold	Cobbold 1858 : 159
Morrhua vulgaris	Belgian coast	van Beneden	van Beneden 1871 : 56
Merlangus carbonarius	England	Cobbold	Cobbold 1858 : 159
Merluccius vulgaris	Warberg	Olsson	Olsson 1867 : 54
Melanogrammus aeglifinus	Woods Hole Region	.....	Sumner, Osborn and Cole 1913 : 586
Microgadus tomocod	Woods Hole Region	.....	Sumner, Osborn and Cole 1913 : 586
Urophycis tenuis	Woods Hole Region	.....	Sumner, Osborn and Cole 1913 : 586
Melanogrammus aeglifinus	Passamaquoddy Bay, New Bruns.	Cooper	Cooper (the present paper)
Melanogrammus aeglifinus	Bay of Fundy, Campobello Id.	Cooper	Cooper (the present paper)
Melanogrammus aeglifinus	Freeport, N. S.	Cooper	Cooper (the present paper)
Gadus callarias	Campobello Id.	Cooper	Cooper (the present paper)
Gadus callarias	Woods Hole Region	V. N. Edwards	Cooper (the present paper)

This species was first described by Goeze (1782:410) under the name of "Der runzlichter Fischbandwurm" and not as *Taenia rugosa*, as indicated by many later writers, including such authorities as Lühe, Braun and Ariola. It was Batsch (1786:208) who gave the specific name on the basis of Goeze's description. The latter, in fact, in a foot-note (p. 410) accepted Pallas' *T. tetragonoceps* to be synonymous with the forms he studied, at least in part, since he recognized that they were at the same time unlike those figured by Pallas after Bloch, from the "Madui-moräne" and the "Rheinlachs." It remained for Rudolphi (1810:42) to give a somewhat more detailed description, which seems to have been accepted by Diesing (1850, 1863) and others, altho Dujar-

din (1845:617) and Cobbold (1858:158) made important additions to the knowledge of the species. Van Beneden (1871:56) erected the new genus, which was later accepted by Lönnberg (1891:75) who used his specific name *gadi* as synonymous with the *B. rugosus* of the earlier writers. Fraipont (1880:267; 1881:12) added to the knowledge of the excretory system. It was not until some time later, however, that Linstow (1889:242) essayed to give a more detailed description of the whole worm, while Lönnberg (1891:75) and Matz (1892:113) by their attention to the anatomy, especially of the reproductive organs, laid the foundation upon which all the writers since have based their conceptions of the species. While the development, especially in its earliest stages, was studied by Schauinsland (1885:527), and later by Saint-Remy (1900:296), the systematic position has since then been dealt with by Blanchard (1894:701), Ariola (1896:272, 274; 1900:432), Riggenbach (1896:223) and Lühe (1899:33; 1900a:47, 96, 101; 1910: 26). Linton (1890:750; 1898:431) is the only writer who has described the species in America.

The dimensions of the species are, according to Lühe (1910:26), 400mm. to 1 meter in length by 2 to 5mm. in maximum breadth; while Ariola (1900: 433) gave the total length of the strobila as from 16 to 97cm. Linton (1890: 751) worked with specimens from the cod, the largest of which measured 655mm. in length by maximum breadth and thickness (posteriorly) of 6 and 2mm., respectively. The largest studied by the writer was a fairly contracted one (No. 301, below) from *Gadus callarias*, 416mm. in length by 7mm. in maximum breadth 100mm. from the incomplete posterior end and 5mm. at the posterior end.

As the names used by Goeze, Batsch and Rudolphi indicate, this species is characterized by its transverse wrinkles or folds, often irregular and complicated by longitudinal grooves and folds anteriorly but regular and corresponding to the internal segmentation posteriorly, and by the general tumid appearance of the strobila due to the very large uterus-sacs gorged with eggs. But most striking of all is the presence of a pseudoscolex which is found embedded in the intestinal coeca or intestinal wall of the host, from which it is extracted only by careful dissection. Goeze (1782:412, Figs. 1, 4 and 5) described a scolex, somewhat elongated, sagittate and irregular but otherwise comparable to that of other bothriocephalids, while Rudolphi (1810:43) does not seem to have found anything of such a structure in *Gadus lota*. Dujardin (1845: 617) was evidently the first to describe the pseudoscolex by saying that, " . . . la partie antérieure [of the strobila] engagée dans l'appendice pylorique forme une sort de bouchon, un cylindre irrégulier, cartilagineux, long de 18mm., large de 4mm., ride ou toruleux et sans ancune trace d'organisation . . . " This description, however, was not recognized by Diesing (1850:590), but he accepted Rudolphi's diagnosis, namely, "Caput subsagittatum, bothriis oblongis lateralibus. . . . " Baird (1853:89) evidently saw two bothria, probably owing to the fact that he was dealing with specimens from *Lota vulgaris* (vide infra). Cobbold (1858:158, 159) was well acquainted with the pseudoscolex, since regarding individuals from the cod ("*Morrhua vulgaris*")

he said "In a cod examined on the 15th of March, 1885, two specimens of *Bothriocephalus rogosus* had severally attained a length of nearly fifteen inches, and their anterior segments for an inch or more downwards, were so firmly impacted within the pancreatic coeca, that it was found impossible to dislodge them without injuring the filamentary head and neck. As if to make the anchorage doubly sure, the cartilaginous thickening of the invaded pancreatic coecum had degenerated into a calcareous and contracted cylinder, twisted upon itself in various ways." Olsson (1867:54) likewise found a pseudoscolex in this species, which he described as being degenerated in *Gadus morrhua* to a yellow, elongated mass which disintegrated on contact with water. It was 18 to 25mm. in length by about one-half a millimetre in diameter, while its position was, as usual, in the wall of a pyloric appendage of the host. He also figured a young strobila from *Gadus aeglifinus*, the scolex of which he considered to have been invaginated. In his new genus and species, *Abothrium gadi*, van Beneden (1871:56) observed the pseudoscolex stating that "Ils ont la tête vers le fond des coecums pyloriques, percent ordinairement les parois et forment, par la gaîne, souvent dure et entortillée comme une tabulaire, une saillie à la surface de cet organe." So far as the writer is aware, he gave the first figure of the structure, as it is commonly met with, encased, however, by the walls of the pyloric coecum in which it was found lodged. Von Linstow (1889:242) described and figured a scolex somewhat similar to that of *A. crassum*, excepting that the apex was hollowed out to form a six-cornered opening which communicated with both bothria. Linton (1890: 750) found pseudoscolices in examples from the codfish, "*Gadus morrhua*," which were much as described by Olsson, since he said that "each of the specimens in this lot has the head and anterior part of the body buried in the pyloric caeca, where they have undergone degeneration to such an extent that no appearance of bothria remains. Around the parts thus enveloped by the caeca is a yellowish waxy deposit, the degenerated tissue of the caeca. This adventitious tissue invested the worm so closely that it would be absolutely impossible for the parasite to free itself from its host." The next important reference to the scolex was by Lönnberg (1891:75) who, while accepting van Beneden's new genus, *Abothrium*, referred the species back to *rugosum* of Batsch, and described the metamorphosis of the anterior end of the strobila into the well-known pseudoscolex, accounting for the various forms, such as figured here. It is noteworthy, however, that he did not state specifically that bothria are present in very young scolices, before this transformation takes place, nor did he give any figures to illustrate the latter. Matz (1892: 114) described and figured a typical scolex for a specimen 36cm. long from *Lota vulgaris*, while Schneider (1903a:9) in delineating a similar structure for the species from the same host, pointed out its great similarity to the scolex of *B. proboscideus* (=*A. crassum*). Perhaps of significance in connection with the question of the metamorphosis of the organ is his statement that "Der ganze Scolex kann sich nämlich durch verschiedene Contraction seiner Muskeln in ein pfeilförmiges, oder fast cubisches, oder sogar sichelförmiges Gebilde

verwandeln." Later Johnstone (1907:170) described the pseudoscolex with considerable detail, finding quite the same conditions as did Linton. On account of never meeting with anything like a typical scolex in adult worms he was led to conclude that "Probably in young codling, recently infected, a stage of the cestode with such a scolex might be found but doubtless with increasing age the changes mentioned above occur, and the normal structure of the head disappears." And lastly, Scott (1909:85) made somewhat similar statements, pointing out that " . . . no satisfactory description of this part of the worm [the pseudoscolex] has yet been published." Thus it is seen that, apart from Olsson's (1867:54) finding in *Gadus aeglifinus* of a possible young stage in the degeneration of the scolex of this species, no one has, as yet, figured in detail its metamorphosis, Lönnberg, however, giving the only description of the process. On the other hand, a typical scolex has been described by several writers, as pointed out above, for what has been taken to be the same species in *Lota vulgaris*, but since there is evidence that the latter is quite different from the species found in marine Gadidae and since the specimens from *Lota maculosa*, studied by the writer, were found to belong to the well known *A. crassum*, a pseudoscolex must be attributed only to adults of *A. rugosum*, at least until the confusion which exists in the literature regarding the form from Lota can be cleared up by further investigation.

Two forms of pseudoscolex which were dissected out by the writer from the pyloric ceca of *Melanogrammus aeglifinus*, the haddock, and *Gadus callarias*, the cod, are shown in figures 35, 36, respectively, the latter being from the largest specimen at hand; while what is doubtless a younger stage in the degeneration of the scolex is shown in figure 34 from the intestine of a haddock. A series of transverse sections of the latter, brought out that the internal anatomy was quite suggestive of a typical scolex, that of *A. crassum*, for example. As shown in the figure, the structure is somewhat flattened in the dorsoventral direction. While there were only faint suggestions of bothria, especially towards the tip, the arrangements of the muscles, nerves and excretory vessels pointed to its being possibly not far removed from the typical form of scolex. This view is supported by the fact that it was found free in the anterior part of the intestine of the haddock, altho, unfortunately, the length of the strobila was not recorded. Among a lot of material taken from several haddock two examples of the true scolex, as it would seem to be at or about the time degeneration sets in, were found. The first one, shown in figure 32, was from the smallest strobila at hand, 22mm. in length, while the other, figure 33, was from an older chain, only the anterior end of which was present with a length of 32mm. and maximum breadth of 2.5. The second is evidently the older from the standpoint of metamorphosis, since it is more conical and less separated from the neck region which is slightly swollen; while the bothria are disappearing as the whole structure is approaching the stage represented by figure 34. In figure 32 are seen somewhat more efficient bothria, but the shape of the organ points to a considerable amount of degeneration having already taken place. The next stage in the degeneration of the scolex

is represented by figure 35. Here the structure is likewise not embedded in the wall of the pyloric cecum in which it is found but free in its lumen, the anchorage for the strobila being obtained by the close approximation of the mouth of the cecum around the narrow neck region and the concomitant swelling of the more distal portions. Furthermore, the indications are that a considerable portion of the anterior end of the strobila is involved in the formation of the organ, especially since it is comparatively large. The final stage is that shown in figure 36, where degeneration has gone on to such an extent that there remains only a filamentous, horny or cartilaginous yellow mass, deeply and firmly embedded in the wall of the cecum. Only the tip is shown, there having been about 6mm. more to the region where it left the host tissues and passed insensibly on to the anterior portion proper of the strobila. The latter showed only faint transverse wrinkles and no distinct division into segments, as is seen, with some irregularity, however, in figure 32. This form of pseudoscolex was found, as described by Olsson, Linton and Johnstone, to be surrounded by the tissue of the cecum degenerated to a yellow waxy mass which, when freed from the surrounding tough tissue, crumbled easily under the dissecting instruments.

The strobila, at first almost cylindrical in shape, gradually becomes wider and more depressed until the maximum breadth near the posterior end is attained. As regards the form of the segments Dujardin said that, ". . . le reste du corps long de 100 à 140mm., large de 2mm. en avant et de 6.5 en arrière, est libre dans l'intestin et formé d'articles tres courts, inégaux ou dilatés ca et là; . . ."; and Linton stated that, "The body is not distinctly segmented at first, but is crossed by innumerable fine wrinkles." While the latter statement is in the main true, and applies particularly to the youngest strobilas, many species show that these rugae, altho much obscured by irregular longitudinal grooves, are simply due to the formation of extremely short segments which correspond proportionately with the much more distinct ones farther back. These segments gradually elongate as they pass backward until the end proglottides are often quadrate or even longer than broad, depending on the degree of contraction or relaxation. Linton gave the length of the segments near the middle of the strobila as from 0.7 to 1.0mm. and posteriorly 0.45, and the thickness as 2mm. The latter was 2.5mm. in the largest specimen examined by the writer. The openings of the uteri on the ventral surface of the strobila form collectively a sort of shallow groove, more pronounced, of course, posteriorly but quite obliterated when the segments are considerably relaxed.

The anatomy of the species was first given careful attention by Linstow (1889:235). Later Lönnberg (1891:75) and Matz (1892:113) published more accurate descriptions to which most of the writers since have referred. That of Lönnberg was found, however, to be most applicable to the material at hand from the cod and the pollack, for Matz was dealing with specimens from *Lota vulgaris* and Linstow apparently confused the two possible species from Lota and the marine Gadidae (*vide infra*).

Linstow included in his conception of the cuticula not only the cuticula proper, which he stated was 3.3μ in thickness, but also the outer clear zone of the subcuticula which he found to be 49μ thick. In the present study the cuticula was found to be about 5μ thick and to be divided into the three zones described by Lönnberg; viz., an outer pseudociliated or ragged layer, occupying almost one-half of the thickness of the whole membrane, a middle homogeneous principal stratum, and an innermost basement membrane which stands out quite distinctly in this species without the use of any special stains. The subcuticula was found to average 0.14mm. in thickness, the clear outer ends of the elongated cylindrical and closely crowded cells being collectively 23μ thick. The whole cortex in transverse sections has a depth of 0.32mm. Small calcareous bodies, quite difficult to distinguish from parenchymatous nuclei, are present as described and figured by Lönnberg. They are oval to elliptical in outline and have a maximum length of 20μ.

The musculature is well developed, and is peculiar in that the sagittal fibres especially retain their myoblasts, which are very easily recognized in sections. "They extend from the dorsal to the ventral surface and are usually attached to the cuticula with their ends, but often fasten on to the walls of the excretory vessels or other organs. Their number rises considerably with increasing age of the proglottis. Since they pass thru the spaces between the bundles of longitudinal muscles, they are partially arranged in fasicles. These muscles have not only a nucleus, but often also surrounding the same a quite large, spindle-shaped protoplasmic mass; and one easily finds the different developmental stages from a spindle-shaped cell to fully developed muscle fibres of typical appearance, where the protoplasm is already transformed and reduced, and only the nucleus persists." They are only slightly more numerous between the sets of reproductive organs than elsewhere. In this region, on the other hand, the transverse series form, as emphasized by Lönnberg, a distinct partition separating all constituents of the genitalia of successive proglottides,the testes and vitelline follicles especially (cf. *A. crassum*). In transverse sections they form a "plate," bounding the medulla externally on each surface, from which a few fibres pass farther out among the bundles of longitudinal muscles. The latter are arranged in two distinct layers, each about 0.15mm. in thickness in the median line, which gradually diminish towards the edges of the strobila where they join thru several small and very irregular bundles. These larger fasicles are further subdivided dorsoventrally into smaller ones of various sizes, all of which are connected longitudinally, however, by strands passing from one to the other, as pointed out by Lönnberg. In the anterior end of the strobila, as one follows them forwards, the fasicles of longitudinal fibres become less and less distinct, but extend to the tip of the scolex, or young pseudoscolex, as the case may be, scattering considerably as they go. In sections thru the structure shown in figure 33, a small number of sagittal and transverse fibres and a very few radial ones, situated between the grooves seen externally proves that it is a scolex, but a poorly developed one, or, as indicated above, one showing early stages in the process of degeneration to form the

pseudoscolex. This latter statement applies in a greater degree to the structure shown in figure 34, since in it still more degeneration is present to the extent that no traces of the radial fibres are to be seen altho there are very shallow bothrial depressions. In each case there appears in the medulla and among the longitudinal muscles near the tip of the organ a considerable amount of a material which takes the Orange-G counterstain very readily. While this is relatively more abundant in the older of the two pseudoscolices in question and intermingled with a good deal of calcareous material, it is confined more to the very tip of the younger organ. It represents possibly the first stages in the development of the yellow horny material seen in the oldest and most degenerate pseudoscolices.

Each of the chief nerve strands has a diameter of about 45μ and is situated usually dorsal to the cirrus and vagina, but occasionally ventral. Linstow (1889:243) gave the diameter as 56μ. Near the scolex of the youngest strobila at hand it was found to be only about 34μ and traversed with transverse and sagittal muscle fibres. Within the scolex the two strands gradually converge and become united between the bothria by several weak and indistinct strands in lieu of a commissure.

The excretory vessels are small and irregular in number and arrangement in the mature segments. Lönnberg gave their number as 10 in young segments and from 30 to 35 in mature proglottides, but anteriorly and in young strobilas, there are two chief canals, as stated by Linstow, close within the nerve strands, accompanied by several smaller ones. They break up in the pseudoscolex into an irregular plexus and posteriorly in the youngest strobilas empty into the terminal vesicle, shown in figure 63.

The first traces of the rudiments of the reproductive organs were seen 5.2mm. from the anterior end of the smallest strobila found, which was 22mm. in length. The genital cloacae alternate irregularly from side to side, altho they may be situated on one side for stretches involving at least five proglottides. Dujardin (1845:617) described them as being unilateral or very irregularly alternating, while Linstow (1889:244) said they were one-sided, and between the middle and hinder one-third of the edges of the proglottides. In the sections made they were found between the first and second thirds, often covered by the edge of the proglottis next ahead and from 35 to 75μ in depth. Since the actual opening is usually closed by the longitudinal contraction of the strobila, it is difficult to distinguish it externally from grooves separating consecutive proglottides or other lateral grooves between irregular rugae. The vagina opens immediately behind the cirrus and slightly ventral, there being no distinct ductus hermaphroditicus. This corresponds with Lönnberg's and Linton's finds, whereas Linstow said that it is opened ahead of the cirrus.

The testes are arranged in two lateral fields between the nerve strands and the uterus and ovary in the median line, and are strictly discontinuous, that is, separated longitudinally into sets corresponding with the other genitalia by the transverse muscular septa between proglottides. Their average maximum length, width and depth are, respectively, 40, 90 and 85μ, thus indicating

that they are usually quite flattened anteroposteriorly. Linstow gave the diameter as 0.06mm. As stated by Lönnberg, they show various stages in the development of spermatozoa quite well. Altho Linstow described them as being arranged in an elongated half-ring on each side, they were found by the writer to occupy all parts of the medulla in the fields indicated, intermingling irregularly with the vitelline follicles, but in general more numerous in the median frontal plane. From 23 to 30 are present in each lateral field, thus making the total number for the proglottis from about 45 to 60. The vas deferens forms an elongated mass of coils in the anterior portion of the proglottis, which extends from the uterus-sac to the cirrus-sac, near which its coils are fewer in number and more openly arranged. The whole mass has a length (transversely) of 0.35mm. by a diameter (longitudinally) of 0.07 to 0.08. As pointed out by Lühe (1900a) the duct forms within the cirrus-sac a proximal winding ductus ejaculatorius—it is often quite dilated—and a distal straight cirrus proper, which occupies half the length of the sac. The cirrus-sac varies in length from 174 to 277μ and in maximum diameter, medially, since the whole is ovoid with the narrow end outward, from 92 to 102μ. Lühe gave the measurements as 220 by 75 to 90μ. As noted by the same writer, myoblastic nuclei form such a thick layer outside of the wall and there are so many parenchymatous nuclei within the sac, that the wall itself is at first difficult to locate in sections. The cirrus proper may have a dorsoventral diameter of 40μ.

The vagina has a diameter of 20μ as it passes the cirrus-sac, and is lined with a comparatively thick cuticula. Lühe stated that the ventral bow in its course is more median than in *A. crassum*, but in the material sectioned the very reverse was found to be the case. The ovary of this species is very conspicuous since it is large (0.6mm.) wide compact and somewhat kidney-shaped; Linstow's measurements are 0.14mm. wide by 0.12 long. There is no distinct isthmus, or, as Lönnberg stated, there is a very broad one, both longitudinally and dorsoventrally, from the middle of the anterior face of which the oviduct arises either towards the dorsal or the ventral surface. The ova are large and conspicuous because of their prominent nuclei which are from 10 to 13μ in diameter, while their nucleoli are about 2.5μ. Linton (1890: 752) gave these data as 8 to 14 and 2.5μ, respectively. The oocapt has a diameter of about 34μ. From it the oviduct proceeds laterally at first, then with a sharp turn back, i.e., "towards the side opposite the genital-opening," it is joined by the vagina just before it makes a second turn towards the dorsal surface of the proglottis (Fig. 109). The viteline follicles are, as stated by Lönnberg, entirely within the parenchymatous muscle-sac—and thus discontinuous longitudinally—altho Lühe (1910:26), probably basing his statements on Matz's (1892:113) description, said that they are ". . . zum Teil noch nach inner von der Längsmuskulatur." They are arranged in two lateral fields corresponding to those occupied by the testes with which they intermingle freely, altho being situated more peripherally. They are somewhat irregular in shape and size, but usually compressed anterposteriorly, and as much as 90μ wide, 30 long and 70 thick. There is a median field free of them

both dorsally and ventrally. Right and left vitelline ducts passing to the median line close to the ventral layer of transverse muscles unite ventrally to form a common duct, which acts as a yolk reservoir. The union of the common vitelline (Fig. 109) duct with the oviduct takes place in the median frontal plane, a little aside from the median line and just beyond the bend in the oviduct before which is located the point of union of the vagina. The shell-gland is quite compact and situated close to the dorsal wall of the medulla. The uterine duct takes only a very few short coils, mostly in the dorsoventral direction close to the median line, before passing into the very capacious uterus-sac. The latter vies with the large ovary in filling up the median portion of the medulla, and measures in mature (not gravid) proglottides, 0.74mm. wide, 0.74 long and 0.37 deep, being obviously quite flattened in the antero-posterior direction as are the other organs. In mature proglottides which are quadrate in shape it may be still somewhat elliptical in outline, as much as 1.6mm. long by 1.3mm. wide, and show distinct lobations; whereas the widest and most gravid joints may be little else than sacs of eggs, the rest of the reproductive system in both cases having almost entirely degenerated. The uterus-sacs were constantly found to be rounded or lobate laterally, as stated by Matz and Lühe. The openings form a somewhat irregular zig-zag row on the ventral surface of the strobila, without, however, being accommodated in a distinct groove.

The eggs, taken from gravid uteri and measured in the formalin in which the strobilas were preserved, were, externally, 80 to 98μ long by 75 to 92 wide; mantle, 67 by 62μ; "ectoderm" (of Schauinsland), 62 by 54μ; and oncosphere, 52 by 40μ. The similar data given by Dujardin, which were considered by Linstow to be not of this species, were: shell, 80 to 110 by 50 to 57μ; "ectoderm," or inner shell, 51 to 57μ; oncosphere, 48 to 50μ. Linstow's figures, copied by Lühe, were 59 by 43μ.

The earliest stages in the development of this species have long been known from the work of Schauninsland (1885:527), who followed it to the escape of the oncosphere enclosed in the non-ciliated mantle. Saint Remy (1900:296-7) thought that he probably saw polar bodies and the male and female pronuclei among other important finds, and came to the conclusion ". . . que les phénomènes sont essentiellement les mêmes chez les Bothriocéphales et chez les Taenia et se résument dans la constitution de deux enveloppes autour de l'embryon hexacanthe." Olsson found a small strobila 22mm. in length in *Gadus aeglifinus*, which he considered to belong to this species; but apart from this there seem to be no other references in the literature to the development of the strobila from the plerocercoid. As stated above, the smallest found by the writer was also 22mm. in length, but no such invagination of the scolex as mentioned by Olsson was observed.

As stated above, there is considerable evidence in the literature of this species to indicate that the form found in marine Gadidae and called *A. gadi* by van Beneden (1871:56) is not the same as that found in the only fresh-water gadid, viz., Lota. In endeavoring to place a number of specimens from *Lota maculosa*, it was found that in many points they agreed with the descrip-

tion given by Matz for *A. rugosum*. The scolices are more or less alike, no pseudoscolex (see below, however) being present; the longitudinal muscles are not in bundles; the genital cloacae are irregularly alternating from side to side; the vagina opens ahead of the cirrus instead of behind; the testes are continuous from proglottis to proglottis; the vitelline follicles are located among the longitudinal muscles and are discontinuous; and the uterus-sacs are rounded laterally. In most of these and in many more points, on the other hand, the form agrees with *A. crassum*, so that the writer is obliged to consider it to belong to that species. Furthermore, a direct comparison of Matz's description with that of Lönnberg brings out many differences. Lönnberg described a pseudoscolex, calcareous bodies, the longitudinal muscles in bundles, the other sets of parenchymatous muscles as above described, the vagina opening behind the cirrus and ventrally, testes discontinuous, vitelline follicles within the parenchymatous muscle-sac and also discontinuous, none of which characters are to be found in Matz's description, but all of which apply to the material at hand from marine Gadidae. It is to be noted here that Lönnberg accepted the specific name *rugosum* of Rudolphi instead of the *gadi* of van Beneden, which as will be seen presently may not be admissable. Going back, then, to the only other and the earliest description of the anatomy of the species, namely, that of Linstow (1889:242-5), similar difficulties and confusion are met with. Linstow gave as hosts for the species, which he called *B. rugosus* Rud., *Gadus aeglifinus*, *G. morrua*, *Merlangus carbonarius*, *M. pollachius*, *Merlucius vulgaris*, *Lota vulgaris*, *L. molva* and *Motella mustela*. Characters in his description not applicable to the material studied are: No pseudoscolex, but scolex of a rather peculiar shape and structure terminally; nerve strand 56μ in diameter; 10 excretory vessels anteriorly arranged in two groups of five each; genital cloacae unilateral, between the middle and hinder thirds of the edge of the proglottis; vagina opening ahead of the cirrus; length of cirrus-sac 0.42mm. (!); ovary 0.14 by 0.12mm.; uterus spherical when obviously young; and eggs 59 to 43μ. Testes with a diameter of 60μ, vagina 16 to 26μ in diameter at the beginning, and two vitelline ducts, besides a few other minor points in the general anatomy, agree, however, with the species as studied by the writer. Thus it is seen there is by no means anything like complete agreement as regards details among the three descriptions by Linstow, Lönnberg and Matz. But this does not seem to have inconvenienced many of the writers since then, notably Ariola (1900:432) and even Lühe (1900a) whose references to the position of the vitelline follicles and the ventral bow in the vagina are at variance with conditions described here; altho Johnstone (1907), Scott (1909) and Nicoll (1910) were obviously dealing with the form described by Lönnberg, Schneider (1903a:7-10) seems to have been the only one who pointed out the differences between the form from Lota and that from marine Gadidae. He said: "*Bothriotaenia rugosa* gleicht sowohl in ihrem Aussehen, als auch in ihrer Anheftungsweise ausserordentlich der Species *B. proboscidea*, die in unseren Lachsen (*Salmo salar*) so massenhaft vorkommt. Trotzdem pflegt man aber seit Rudolphi, soviel mir bekannt, immer die in Lota meist vorkom-

mende Form als eine getrennte Species auf zufassen unter dem Namem '*rugosa*' (*Bothriocephalus rugosus* Rud. = *Dibothrium rugosum* Diesing, u.s.w.), obgleich die unterscheidenden Merkmale zwischen *B. proboscidea* und *B. rugosa*, die Riggenbach in seinen 'Bemerkungen ueber das Genus *Bothriotaenia* Railliet' übersichtlich zusammenstellt, recht unbedeutend sind und vielleicht doch noch in Rahmen der Variationsbreite einer einzigen Species untergebracht werden können;" and, as regards the latter, in a footnote: "Die von M. Lühe . . . als Unterscheidungsmerkmal vorgeschlagene Lage der Dotterstöcke zum Theil (*B. rugosa*), bzw. auschliesslich (*B. proboscidea*) zwischen den Längsmuskeln, scheint mir auch nicht genugend constant sein, um als Speciesmerkmal verwandt werden zu können." For material from *Lota vulgaris* Schneider described a scolex and segments both similar, as he pointed out, to those of *B. proboscidea* (=*A. crassum*). The arrangement of the genital cloacae, irregularly alternating but unilateral for long stretches, the openings of the uteri in a longitudinal furrow, the early form of the uterus-sac and the size of the eggs (64.5 by 50 to 52μ), as described by the same worker, all agree with *A. crassum* as studied by the writer. In conclusion Schneider said: "Uebrigens habe ich, wie gesagt, auch an die Examplaren aus dem Museum keine Pseudoscolexbildung bemerkt und zweifle daran, dass *B. rugosa* und *B. gadi* ein und dieselbe Art sind," and further, "Es ist mir übrigens bisher noch nicht gelungen, *B. rugosa* oder *B. gadi* in *Gadus morrhua* des Finnischen Meerbusens aufzufinden, obgleich ich zahlreiche Exemplare des Dorsches seciert habe, und obgleich *B. rugosa* in *Lota vulgaris* hier oft genug vorkommt. Auch das scheint gegen die Identität der Species *B. rugosa* mit *B. gadi* zu sprechen."

Thus it is seen that there is considerable detailed evidence that the species from Lota is not the same as that from the marine hosts. One must then go back of Linstow's time in order to determine, if possible, what is the correct name for the latter. Next in retrogressive order is van Beneden's (1871:56) description of *A. gadi*, confined to a short footnote which deals with little more than the pseudoscolex. So far as it goes this agrees with Lönnberg's *A. rugosum* and with the material studied by the writer. Olsson (1867:54) was obviously dealing with the same form which he reported from marine hosts only. Diesing (1863 and 1850) copied from Rudolphi, while Cobbold (1858) had the marine form before him, and Baird (1853) had the fresh-water form. In spite of Linstow's objection the writer feels certain that Dujardin (1845) also had the species dealt with here, especially since his measurements of the eggs come nearest to those observed than do those of any other writer. It remains then to enquire into Rudolphi's finding and description, as Leuckart (1819:57) copied from him altho at the same time remarking that "Ist am nächsten mit den *B. proboscideus* verwandt, und, wenn er nicht eine Art mit diesem ausmacht zwischen *B. proboscideus* und *B. sagittatus* zustellen." For *B. rugosus* Rudolphi (1810:42) described a scolex, comparable to that of his *B. proboscideus* and to Linstow's description and figure of the organ, no neck, and segments "primi angusti, fere quadrati, insequentes latitudinis ratione habita brevissimi, saepeque inequales, vel hinc inde angustiores; margines obtusi crassiusculi."

This, with "neque ovaria, neque foramina articulorum vidi . . . " and the further fact that he obtained his specimens from *Gadus lota* (=*Lota vulgaris*), leads the writer to believe that he was not dealing with the form present in marine hosts but with a form which, if not identical with *A. crassum* (=his *B. infundibuliformis* and *B. proboscideus*), was very close to it. One must then go back farther to Batsch (1786:208) where the species *T. rugosa* was named on the basis of Goeze's (1782:410) description of "Der runzlichter Fischbandwurm" from *Gadus mustela* (=*Motella mustela*), the marine five-breared rockling of Europe, which the latter called *T. tetragonoceps* Pallas, with some doubts, however, as discussed under the next species dealt with here. Batsch gave the following diagnosis of *T. rugosa:*

"Taenia (larvata) capite conico cum corpore subconfluente, papillis lateraliter adnatis usque ad apicem capitis, eisque binis: articulis brevissimis, dilatatis, corpore serrato."

He used Goeze's figures 1 to 4 and pointed out that he (Goeze) recognized differences between his specimens and Pallas' *T. tetragonoceps*, for "Er rechnet beyde Würmer fur eine Art, und die Glieder nebst dem ganzen Korper haben viel Gleichheit, auch die äussere Gestalt des Kopfs. Doch sind bey diesem letztern die Saugblasen bey weiten nicht so deutlich gezeichnet, und stellen vielmehr, wie sich Götze ausdrückt, zwey Backenbarte vor. Die Furche auf dem Korper ist auch vorhanden, nur scheint der Korper mehr gestreckt, und am Rande mehr zackig zu seyn." Consequently the correct name of the species depends on whether Goeze's description, augmented by Batsch's contributions, is considered to be applicable to the material at hand. The largest of Goeze's specimens measured in warm water a yard and half in length by scarcely one-half a line in breadth; but the latter is decidedly at variance with his figures 1 and 2 which he said were drawn in "natürlicher Grösse," in which case the width would be from 7 to 15 lines and the scolex about 17.5 lines in length! For these large specimens—even tho only the first set of measurements were taken into consideration—he described and figured nothing of diagnostic value other than a scolex provided with two bothria pretty much of the ordinary type, behind this a "distinctly jointed" and "almost cylindrical" neck and along both surfaces of the posterior closely crowded segments a median longitudinal furrow, all of which characters more nearly agree with the *proboscideus* type of *A. crassum* rather than with the *A. rugosum* described here. And since the latter is clearly not *T. tetragonoceps* Pallas as described by Batsch (1786:204), the only course that seems open is to refer the species to van Benden's *Abothrium gadi.* However, in view of the fact that no material from the European ling (*Lota vulgaris*) was available for a comparative study, the writer does not feel justified in taking this step, but here retains at least tentatively the specific name *Abothrium rugosum* (Batsch 1786), nec *A. rugosum* Goeze 1782.

The material studied consisted of lots 295, 296, 297, 298, 299, 300, and 302 from *Melanogrammus aeglifinus* (L.), the haddock, and 301 from *Gadus callarias*, the cod in the writer's collection; and 17.53 in the collection of the University of Illinois, also from the cod.

ABOTHRIUM CRASSUM (Bloch 1779)

[Figs. 37-42, 50-54, 64, 77, 92]

1779	*Taenia crassa*	Bloch	1779 : 545
1780	*Taenia salmonis*	Müller	1780 : 179, 202
1781	*Taenia tetragonoceps* (part.)	Pallas	1781 : 87
1782	*Taenia capite truncato*	Bloch	1782 : 410
1782	"Der runzlichter Fischbandwurm"	Goeze	1782 : 410
1782	*Taenia proboscis suilla*	Goeze	1782 : 417
1786	*Taenia tetragonoceps*	Batsch	1786 : 204
1786	*Taenia proboscidea*	Batsch	1786 : 212
1790	*Taenia salmonis*	Gmelin	1790 : 3080
1790	*Taenia salvelini*	Schrank	1790 : 125
1793	*Taenia salvelini*	Schrank	1793 : 141
1795	*Taenia salmonis*	Rudolphi	1795 : 17
1802	*Taenia salmonis*	Bosc	1802 : 308
1802	*Taenia proboscidea*	Rudolphi	1802 : 106
1803	*Rhytis salvelini*	Zeder	1803 : 292
1810	*Bothriocephalus proboscideus*	Rudolphi	1810 : 39
1810	*Bothriocephalus infundibuliformis*	Rudolphi	1810 : 46
1816	*Bothriocephalus proboscideus*	Lamarck	1816 : 582
1819	*Bothriocephalus proboscideus*	Rudolphi	1819 : 137, 472
1819	*Bothriocephalus infundibuliformis*	Rudolphi	1819 : 137, 473
1819	*Bothriocephalus proboscideus*	Leuckart	1819 : 38
1819	*Bothriocephalus infundibuliformis*	Leuckart	1819 : 42
1843	*Bothriocephalus salmonis umblae*	Koelliker	1843 : 91
1844	*Bothriocephalus proboscideus*	Bellingham	1844 : 252
1844	*Bothriocephalus infundibuliformis*	Bellingham	1844 : 253
1845	*Bothriocephalus proboscideus*	Dujardin	1845 : 615
1845	*Bothriocephalus infundibuliformis*	Dujardin	1845 : 616
1846	"Bothriocephalus du Saumon"	Blanchard	1847 : 116
1850	*Dibothrium proboscideum*	Diesing	1850 : 590
1850	*Dibothrium infundibuliforme*	Diesing	1850 : 590
1853	*Bothriocephalus proboscideus*	Baird	1853 : 88
1853	*Bothriocephalus infundibuliformis*	Baird	1853 : 88
1863	*Dibothrium proboscideum*	Diesing	1863 : 242
1863	*Dibothrium infundibuliforme*	Diesing	1863 : 242
1867	*Bothriocephalus proboscideus*	Olsson	1867 : 53
1871	*Bothriocephalus proboscidea*	van Beneden	1871 : 69
1878	*Bothriocephalus infundibuliformis*	Linstow	1878 : 263
1884	*Bothriocephalus infundibuliformis*	Zschokke	1884 : 21
1889	*Bothriocephalus suecicus*	Lönnberg	1889 : 35
1892	*Bothriocephalus infundibuliformis*	Matz	1892 : 110
1893	*Bothriocephalus infundibuliformis*	Olsson	1893 : 17
1893	*Bothriocephalus proboscideus*	Olsson	1893 : 17
1894	*Bothriotaenia infundibuliformis*	Blanchard	1894 : 701
1896	*Bothriotaenia infundibuliformis*	Ariola	1896 : 280
1896	*Bothriotaenia infundibuliformis*	Riggenbach	1896 : 223
1899	*Abothrium crassum*	Lühe	1899 : 39
1900	*Bothriotaenia proboscidea*	Ariola	1900 : 433
1900	*Abothrium crassum*	Lühe	1900a : 97
1909	*Bothriocephalus proboscideus*	Scott	1909 : 78
1910	*Abothrium crassum*	Lühe	1910 : 26
1910	*Abothrium crassum*	Ward	1910 : 1184

Specific diagnosis: With the characters of the genus. Large cestodes with maximum length, breadth and thickness of 870, 6 and 2mm., respectively. Scolex variously shaped; usually rounded posteriorly and truncated anteriorly; with prominent bothria and terminal disc. First segment may or may not be elongated to form a short neck. Proglottides at first broad and short or more quadrate, cuneate or infundibuliform in shape; in the middle of the strobila, five or more times broader than long; posteriorly, quadrate or as long as broad. Usually a median longitudinal groove down each surface of the strobila formed by emarginations on the posterior borders of the segments.

Cuticula 4 to 6μ thick, subcuticula 40 to 100μ. Calcareous bodies (?) absent in adult strobilas. Longitudinal muscles not in bundles; no muscular septa between proglottides. Nerve strands 25 to 40μ in diameter, dorsal to inner end of cirrus-sac. 12 chief excretory vessels, 6 on each surface just within the transverse muscles, reduced to 6 or 8 anteriorly.

Genital cloaca irregularly alternating, but unilateral for long stretches; from one-third to one-half way along the margin of the proglottis. Vagina opens ahead of and slightly ventral to the cirrus; no distinct hermaphroditic duct.

Testes within the nerve strands, pseudostratified, continuous from joint to joint; elongated dorsoventrally, 95 to 115 by 70 to 100μ; 40 to 150 in number. Vas deferens lateral, elongated, with few coils before entering the cirrus-sac, 350 to 600 by 100 to 180μ in dimensions. Cirrus-sac ovoid with narrow end outward, 130 to 380 by 60 to 150μ. Cirrus proper an almost straight tube in outer half of sac.

Ovary comparatively small, irregular or somewhat lobed, with thick isthmus, 0.8mm. wide by 0.13 long. Oocapt 40μ in diameter. Usually two ventral vitelline ducts unite to form a common duct which does not act as a reservoir. Vitelline follicles irregular in shape and size, among the longitudinal muscles or outside of them, discontinuous. Shell-gland small, compact, dorsal. Uterine duct with only a few coils near the median line. Uterus-sac transversely elliptical or somewhat quadrate and slightly lobed, rounded laterally filling up almost the entire proglottis when gravid; opening in the median line opposite emarginations of segments ahead.

Eggs, 45 to 115 by 30 to 75μ; ovoid or ellipsoid in shape.

Habitat: In the pyloric coeca and intestine of the host.

HOST	LOCALITY	COLLECTOR	AUTHORITY
Salmo salar	.....	Borke	Goeze 1782 : 417
Salmo salar	Gryphswald	Rudolphi	Rudolphi 1819 : 137
Salmo salar	Ireland	Bellingham	Bellingham 1844 : 253
Salmo salar	Paris	Dujardin	Dujardin 1845 : 615
Salmo salar	.....	M. C. V.	Diesing 1850 : 590
Salmo salar	.....	Siebold & Johnston (Coll. Brit. Mus.)	Baird 1853 : 88

ABOTHRIUM CRASSUM (Bloch 1779)

[Figs. 37-42, 50-54, 64, 77, 92]

1779	*Taenia crassa*	Bloch	1779 : 545
1780	*Taenia salmonis*	Müller	1780 : 179, 202
1781	*Taenia tetragonoceps* (part.)	Pallas	1781 : 87
1782	*Taenia capite truncato*	Bloch	1782 : 410
1782	"Der runzlichter Fischbandwurm"	Goeze	1782 : 410
1782	*Taenia proboscis suilla*	Goeze	1782 : 417
1786	*Taenia tetragonoceps*	Batsch	1786 : 204
1786	*Taenia proboscidea*	Batsch	1786 : 212
1790	*Taenia salmonis*	Gmelin	1790 : 3080
1790	*Taenia salvelini*	Schrank	1790 : 125
1793	*Taenia salvelini*	Schrank	1793 : 141
1795	*Taenia salmonis*	Rudolphi	1795 : 17
1802	*Taenia salmonis*	Bosc	1802 : 308
1802	*Taenia proboscidea*	Rudolphi	1802 : 106
1803	*Rhytis salvelini*	Zeder	1803 : 292
1810	*Bothriocephalus proboscideus*	Rudolphi	1810 : 39
1810	*Bothriocephalus infundibuliformis*	Rudolphi	1810 : 46
1816	*Bothriocephalus proboscideus*	Lamarck	1816 : 582
1819	*Bothriocephalus proboscideus*	Rudolphi	1819 : 137, 472
1819	*Bothriocephalus infundibuliformis*	Rudolphi	1819 : 137, 473
1819	*Bothriocephalus proboscideus*	Leuckart	1819 : 38
1819	*Bothriocephalus infundibuliformis*	Leuckart	1819 : 42
1843	*Bothriocephalus salmonis umblae*	Koelliker	1843 : 91
1844	*Bothriocephalus proboscideus*	Bellingham	1844 : 252
1844	*Bothriocephalus infundibuliformis*	Bellingham	1844 : 253
1845	*Bothriocephalus proboscideus*	Dujardin	1845 : 615
1845	*Bothriocephalus infundibuliformis*	Dujardin	1845 : 616
1846	"Bothriocephalus du Saumon"	Blanchard	1847 : 116
1850	*Dibothrium proboscideum*	Diesing	1850 : 590
1850	*Dibothrium infundibuliforme*	Diesing	1850 : 590
1853	*Bothriocephalus proboscideus*	Baird	1853 : 88
1853	*Bothriocephalus infundibuliformis*	Baird	1853 : 88
1863	*Dibothrium proboscideum*	Diesing	1863 : 242
1863	*Dibothrium infundibuliforme*	Diesing	1863 : 242
1867	*Bothriocephalus proboscideus*	Olsson	1867 : 53
1871	*Bothriocephalus proboscidea*	van Beneden	1871 : 69
1878	*Bothriocephalus infundibuliformis*	Linstow	1878 : 263
1884	*Bothriocephalus infundibuliformis*	Zschokke	1884 : 21
1889	*Bothriocephalus suecicus*	Lönnberg	1889 : 35
1892	*Bothriocephalus infundibuliformis*	Matz	1892 : 110
1893	*Bothriocephalus infundibuliformis*	Olsson	1893 : 17
1893	*Bothriocephalus proboscideus*	Olsson	1893 : 17
1894	*Bothriotaenia infundibuliformis*	Blanchard	1894 : 701
1896	*Bothriotaenia infundibuliformis*	Ariola	1896 : 280
1896	*Bothriotaenia infundibuliformis*	Riggenbach	1896 : 223
1899	*Abothrium crassum*	Lühe	1899 : 39
1900	*Bothriotaenia proboscidea*	Ariola	1900 : 433
1900	*Abothrium crassum*	Lühe	1900a : 97
1909	*Bothriocephalus proboscideus*	Scott	1909 : 78
1910	*Abothrium crassum*	Lühe	1910 : 26
1910	*Abothrium crassum*	Ward	1910 : 1184

Specific diagnosis: With the characters of the genus. Large cestodes with maximum length, breadth and thickness of 870, 6 and 2mm., respectively. Scolex variously shaped; usually rounded posteriorly and truncated anteriorly; with prominent bothria and terminal disc. First segment may or may not be elongated to form a short neck. Proglottides at first broad and short or more quadrate, cuneate or infundibuliform in shape; in the middle of the strobila, five or more times broader than long; posteriorly, quadrate or as long as broad. Usually a median longitudinal groove down each surface of the strobila formed by emarginations on the posterior borders of the segments.

Cuticula 4 to 6μ thick, subcuticula 40 to 100μ. Calcareous bodies (?) absent in adult strobilas. Longitudinal muscles not in bundles; no muscular septa between proglottides. Nerve strands 25 to 40μ in diameter, dorsal to inner end of cirrus-sac. 12 chief excretory vessels, 6 on each surface just within the transverse muscles, reduced to 6 or 8 anteriorly.

Genital cloaca irregularly alternating, but unilateral for long stretches; from one-third to one-half way along the margin of the proglottis. Vagina opens ahead of and slightly ventral to the cirrus; no distinct hermaphroditic duct.

Testes within the nerve strands, pseudostratified, continuous from joint to joint; elongated dorsoventrally, 95 to 115 by 70 to 100μ; 40 to 150 in number. Vas deferens lateral, elongated, with few coils before entering the cirrus-sac, 350 to 600 by 100 to 180μ in dimensions. Cirrus-sac ovoid with narrow end outward, 130 to 380 by 60 to 150μ. Cirrus proper an almost straight tube in outer half of sac.

Ovary comparatively small, irregular or somewhat lobed, with thick isthmus, 0.8mm. wide by 0.13 long. Oocapt 40μ in diameter. Usually two ventral vitelline ducts unite to form a common duct which does not act as a reservoir. Vitelline follicles irregular in shape and size, among the longitudinal muscles or outside of them, discontinuous. Shell-gland small, compact, dorsal. Uterine duct with only a few coils near the median line. Uterus-sac transversely elliptical or somewhat quadrate and slightly lobed, rounded laterally filling up almost the entire proglottis when gravid; opening in the median line opposite emarginations of segments ahead.

Eggs, 45 to 115 by 30 to 75μ; ovoid or ellipsoid in shape.

Habitat: In the pyloric coeca and intestine of the host.

HOST	LOCALITY	COLLECTOR	AUTHORITY
Salmo salar	.....	Borke	Goeze 1782 : 417
Salmo salar	Gryphswald	Rudolphi	Rudolphi 1819 : 137
Salmo salar	Ireland	Bellingham	Bellingham 1844 : 253
Salmo salar	Paris	Dujardin	Dujardin 1845 : 615
Salmo salar	.....	M. C. V.	Diesing 1850 : 590
Salmo salar	.....	Siebold & Johnston (Coll. Brit. Mus.)	Baird 1853 : 88

HOST	LOCALITY	COLLECTOR	AUTHORITY
Salmo salar	Warberg	Olsson	Olsson 1867 : 53
Salmo salar	Belgian coast	van Beneden	van Beneden 1871 : 69
Salmo salar	Warnemünde	Zschokke	Braun 1891 : 55
Salmo salar	Näset	Olsson	Olsson 1893 · 17
Salmo salar	Rhine R., Basel	Zschokke	Zschokke 1896 : 776
Salmo salar nobilis	Murman-Küste	Zool. Mus., Kais Akad. Wiss., Petrograd	Linstow 1903 : 20
Salmo salar sebago	Lake Sebago, Me	Ward	Ward 1910 : 1184
Salmo alpinus		Mus Vienn.	Rudolphi 1819 : 137
Salmo alpinus	Jenitland	Olsson	Olsson 1876 : 149
Salmo alpinus	Lakes Nackten, Storsjön, Locknesjon	Olsson	Olsson 1893 : 17
Salmo carpio	L. Garda, Italy	Ninni	Stossich 1890 : 7
Salmo caspius	Karabugas-Strasse	Maximovic	Linstow 1903 · 20
Salmo fario	Ireland	Bellingham	Bellingham 1844 252
Salmo fario	Rome	Condorelli	Ariola 1900 . 435
Salmo fario	Vyg-Fluss	Danilevskij	Linstow 1903 · 20
Salmo hucho		Mus Vienn. and Bremser	Rudolphi 1819 : 472
Salmo lacustris	Benaco	Largaiolli	Ariola 1900 · 435
Salmo namaycush	Shoal Id., Lake Superior	Milner	Ariola 1900 : 435
Salmo salvelinus		Schrank	Stiles & Hassall 1912 : 402
Salmo salvelinus		Zeder	Stiles & Hassall 1912 : 403
Salmo salvelinus		Mus Vienn.	Rudolphi 1819 · 137
Salmo salvelinus		Diesing	Diesing 1850 · 591
Salmo siscowet	Outer Id., Lake Superior	Milner	Ariola 1900 . 435
? *Salmo thymallus*		Coll Vienn.	Leuckart 1819 : 43
Salmo thymallus vexillifer		M. C. V.	Diesing 1850 : 591
Salmo trutta	Ireland	Bellingham	Bellingham 1844 · 253
Salmo trutta		Coll. Brit. Mus	Baird 1853 : 88
Salmo trutta	Lakes Stòrsjon, Hålen, Refundssjon, Sallsjón, & Ockesjon, Jemtland	Olsson	Olsson 1893 : 17
Salmo trutta	Murman-Küste	Zool. Mus. d. Kais. Akad. Wiss , Petrograd	Linstow 1910 : 281
Salmo umbla		M. C. V.	Diesing 1850 : 591
Salmo umbla		Zschokke	Zschokke 1884 : 21
Coregonus fera		Zschokke	Zschokke 1884 : 21
Coregonus lavaretus	Lakes Storsjön and Nälden	Olsson	Olsson 1893 : 17

HOST	LOCALITY	COLLECTOR	AUTHORITY
Coregonus oxyrhynchus maraena	Warberg	Olsson	Olsson 1867 : 53
Trutta fario	Genfersee, Basel	Zschokke	Zschokke 1896 : 776
Trutta lacustris	Rhine R., Basel	Zschokke	Zschokke 1896 : 776
Trutta lacustris	Bodensee	Hofer	Hofer 1904 : 221
Trutta salar	East Prussia	Muehling	Muehling 1898 : 35
Trutta trutta	Warnemünde	Zschokke	Braun 1891 : 55
Trutta variabilis	.....	Zschokke	Zschokke 1884 : 21
Thymallus vulgaris	.....	Zschokke	Zschokke 1884 : 21
Thymallus vulgaris	Störsjön, Jemtland	Olsson	Olsson 1893 : 17
Thymallus vulgaris	Baikal-See	Zool. Mus. d. Kais. Akad. Wiss., Petrograd	Linstow 1903 : 20
Esox lucius	.....	Zschokke	Zschokke 1884 : 21
Perca fluviatilis	.....	Zschokke	Zschokke 1884 : 21
Osmerus operlanus	Bönan, Gestricia, Gulf of Bothnia	Olsson	Olsson 1893 : 17
Clupea harengus	Ostsee	Schneider	Schneider 1902 : 28
Lota vulgaris	Störsjön, Jemtland	Olsson	Olsson 1893 : 17
Lota vulgaris	Dvina-Fluss	Danilevskij	Linstow 1903 : 20
"Trout"	Loch Tay	Williamson	Scott 1909 : 78
Salmo salar	St. Andrews, N.B., Bay of Fundy	Cooper	Cooper (the present paper)
Cristivomer namaycush	Giants Tomb Id., Georgian Bay, L. Huron	Cooper	Cooper (the present paper)
Cristivomer namaycush	Port Credit, Ont., Lake Ontario	Cooper	Cooper (the present paper)
Cristivomer namaycush	L. Temagami, Ont.	H. B. Ward	Cooper (the present paper)
Cristivomer namaycush	Charlevoix, Mich.	H. B. Ward	Cooper (the present paper)
Cristivomer namaycush	Pentwater, Mich.	H. B. Ward	Cooper (the present paper)
"Lota lota"	Charlevoix	H. B. Ward	Cooper (the present paper)
Lota maculosa	Port Credit	Cooper	Cooper (the present paper)
Lota maculosa	Potaganissing, and Sitgreaves Bays, L. Huron	G. R. LaRue	Cooper (the present paper)
Lota maculosa	Charlevoix, Mich.	Cooper	Cooper (the present paper)
Coregonus clupeiformis	Giant's Tomb Island	Cooper	Cooper (the present paper)
Coregonus clupeiformis	Potaganissing Bay, L. Huron	G. R. LaRue	Cooper (the present paper)
Salvelinus fontinalis	Harrietta, Mich.	G. R. LaRue	Cooper (the present paper)

This species, originally given the specific name of *Taenia crassa* by Bloch (1779:545), was on the one hand confused with *A. rugosum* and on the other hand given the new name *Taenia proboscis suilla* by Goeze (1782:410 and 417, resp.) according as it was found in Gadus or in *Salmo salar*. This confusion was evidently due to the fact that the latter followed Pallas (1781) in calling it *T. tetragonoceps*; for, as he said, "Pallas setzt ihn mit Recht l.c. unter die neuen Arten. [In the footnote, he considered that *T. tetragonoceps* Pallas, *Taenia crassa* Bloch and *T. capite truncato* Bloch were all synonymous]. Er hat ihn in verschiedenen Fischen, im Rhein- and Elb-lachs, auch in kleinem Lachs (Eriox) am grössten im Babeljau, im Dorsch, in Schollen und Aalen; der Graf von Borke in der Teufelsmoraene und Meergrappe; D. Bloch in der Madui-Moraene und im Rheinlachs gefunden." But in spite of this, he expressed doubt on the synonym of the forms from the Gadidae and from the Salmonidae in the next paragraph: "Da aber die Zeichnungen des Pallas von der Abbildung des D. Blochs von diesem Wurm, so sehr verschieden sind; und die letztere die nämliche ist, die mir der Graf von Borke von dem Fischwurm aus dem Aal zugeschickt hat; so vermuthe ich fast, dass es dennoch verschiedene Arten sind;" and immediately supported this contention by comparing Loewenhoek's "Vermes multimembres ex Anguilla" (vide supra = *B. claviceps*) with Palla s form and pointing out differences. Elsewhere (p. 417) he described under the name "Der Schweinrüssel *Taenia Proboscis Suilla*: articulis foliaceo sinuosis." from *Salmo salaris* L. what was without doubt the *B. proboscidea* of later writers. Goeze's diagnosis of this form is as follows:

"Vom Graf von Borke aus einem siebenpfundigem Lachs (*Salmo salaris* L.). Besonders in den Blinddarmen. Der Kopf wie ein Schweinsrüssel, mit vier länglichten flachen Saugblasen. Gleich hinter dem Kopfe, ohne Hals, die Blätterförmigen ausgeschweiften Glieder. Ich will nicht mit Gewissheit behaupten, dass dies eine ganz besondere Art sey. So hatte ihn der Graf von Borke gesehen und der Kopf unterscheidet sich von andern. Diese Zeichnung, die ich hier liefre, war auch dem Hr. D. Bloch, mitgetheilet."

The explanation (p. 418) of the figures 1 and 2, Table XXXIV, here referred to, indicate, incidentally, that he considered the bothria to be lateral instead of dorsoventral in position. Rudolphi (1810:39, 46, resp.) gave the first diagnoses of the two species, viz., *B. proboscideus* and *B. infundibuliformis*, which were later united by Zschokke (1884:21) and Matz (1892:110) into one species, now known as *A. crassum*. Rudolphi's later (1819:137) condensed diagnoses are here given for the sake of comparison:

"2. Bothriocephalus proboscideus R.

B. capite bothriisque marginalibus oblongis, collo nullo, corpore depresso medio sulcato, articulis brevissimis, antrorsum attenuatis."

"5. Bothriocephalus infundibuliformis R.

B. capite bothriisque oblongis, collo nullo, articulis variis, primis rugaeformibus, sequentibus subinfundibuliformibus, reliquis brevioribus." In the same work (pp. 472, 473) he pointed out resemblances between these two species in that, as regards *B. proboscideus*, "Specimina maxima in intestinis *Salmonis*

Huchonis reperta, quae Bremserus mecum communicavit ad speciem insequentem (praesertim parte anteriore) transitum faciunt;" and under *B. infundibuliformis*, the following species, concerning the same specimens: ". . . quae parte anteriore cum B. proboscideum arguunt." Leuckart (1819:38, 42) accepted Rudolphi's two species and gave good figures of the scolices and anterior ends of the same; but recognized two forms of *B. proboscideus*, viz.,

"a. Collo nullo; corpore medio sulcato.

Habitat in Salmonis salaris appendicibus pyloricis.

b. Collo brevissimo; corpore medio non sulcato.

Habitat in Salmonis Huchonis intestinis."

He further pointed out and corrected the errors of Pallas, Bloch and Goeze regarding the scolex, and concerning *B. infundibuliformis* said : "Kömme *B. proboscideus* am nächsten, ist aber gewiss eine von ihm verschiedene Art, obgleich Bremser . . . sagt, dass er beide Arten nicht gern trennen mögte." Bellingham (1844:252) was evidently the first to comment on the relation between the number of individuals of this species and the condition of the host, when he said, "I have found the *B. proboscideus* in such numbers in the intestines and pyloric appendages of the *Salmo salar* as almost completely to block up these parts, which contained nothing besides but a white tenacious mucus. The fish in which they were most numerous were amongst the finest in the market; which would help to prove, that in these animals at least, the presence of entozoa in the alimentary canal is not to be regarded as the result of disease." He pointed out the great variation due to different states of contraction or relaxation of the scolex and segments and also that *B. infundibuliformis* from *Salmo trutta* " . . . resembles generally the *B. proboscideus*, but differs from it in some respects." While Olsson (1867:53) and Van Beneden (1871:69) found only *B. proboscideus*, others recognized Rudolphi's two species; so that it remained for Zschokke (1884:21-25) to compare the two species in detail and point out that they must be considered only different forms of the same species. Later investigations into the anatomy by Matz (1892:110), who, however, studied only the *proboscideus* form from *Trutta trutta* and *Salmo salar*, were considered to have established this contention, altho Olsson (1893: 17) still reported both of the older species with some doubt as to the use of the name *B. infundibuliformis*. Blanchard (1894:701), Ariola (1896:280), and Riggenbach (1896:223) evidently accepted only the combination *Abothrium crassum* (Bloch) which is now generally accepted. Ariola (1900:433), however, called the species *Bothriotaenia proboscidea* (Batsch), thus disregarding the fact that Batsch (1786:212) renamed Bloch's *T. crassa*.

In general appearance the material studied agreed with the descriptions of both *B. proboscideus* and *B. infundibuliformis* of the early writers; for the former type from *Salmo salar*, the Atlantic salmon, would at first sight be considered to belong to a different species from those taken from the fresh-water hosts. The largest of the latter was one from a specimen of *Cristivomer namaycush*, which measured 856mm. in length by a maximum breadth of 3mm., while the largest from the salmon measured 754mm. in length, 6mm. in maximum

breadth and about 2mm. in thickness. One from *Coregonus clupeiformis* measured 292 by 1.8mm. and another 185 by 2mm., while those from *Lota maculosa* were all small, fragmentary and mostly immature. The dimensions are according to Lühe (1910:27) about 300mm. in length by about 1.5 to 3.5 in breadth; to Zschokke (1884:23) 350 by 4mm.; and to Ariola (1900:435) 250 to 400 by 2 to 4mm. Thus it is seen that as regards size the two forms are more nearly alike in Europe than here. Consequently one is not surprised to read in the comparison by Zschokke, "En effet je trouvais souvent dans le même poisson, même dans le même appendice pylorique des exemplaires dont les uns se rapprochaient évidemment du *Bothriocephalus proboscideus*, tandis que les autres présentaient les caractères de l'*infundibuliformis*. Souvent aussi les caractéres des deux espèces étaient réunis sur un seul individu, par exemple le cou assez prononcé avec des proglottis en forme de bâtons, ou point de cou avec les proglottis *infundibuliformes* bien caracterisés."

In preserved material the scolex assumes a great variety of shapes, from the much elongated form with the "neck" of Olsson (1893:17) and earlier writers shown in figure 37, to that from *Salmo salar*, shown in figure 39. Altho the latter is much the largest and apparently quite different from the former, scolices quite like it excepting for size were seen in specimens from the lake trout, and all stages between these two extremes were observed. The form with the neck, it may be said, is much more common in the youngest strobilas and plerocercoids (Figs. 53, 54). Regarding this structure Zschokke (1884:24) said that, "à l'état de forte contraction le cou disparaît presque complétement." Those from *Lota maculosa*, the ling, need special mention since, as shown in figure 38, the terminal disc and anterior half of the organ of fixation is in many instances greatly swollen to form a sort of pseudoscolex which is usually found imbedded in the walls of the pyloric ceca of the host or often simply protruding into the lumina of the ceca. But this modification was found only in the older strobilas; in the younger chains the scolex is as shown in figures 41, 42, which are drawn to the same scale. The largest with this first form of scolex was 30mm. in length by 1.2 in breadth, while the shortest with the swollen end was 20 by 1.0mm.; so that somewhere between the lengths of 20 and 30mm. the imbedding of the scolex with the concomitant enlargement of the terminal disc takes place. Several intermediate stages were seen, and the swollen scolices were varied in shape and degree of intactness. The latter might seem to point to the condition being due to mechanical or physical means, but this is offset by the fact that the material was in good histological condition when sectioned.

The segments also vary considerably in shape, the first ones being in specimens from fresh-water hosts distinctly cuneate or infundibuliform and slightly broader than long, the middle ones relatively broader and shorter, and the posterior segments especially in the older chains very short and crowded. Furthermore, in larger and older strobilas of the fresh-water form the posterior kind of segment, that is, the very short broad form, is found relatively farther forward, and the hinder end of the same quite similar, excepting for size, to

the worms from the salmon. In the latter the segments, as shown in figure 39, are at first short and broadly cuneate and at once become still shorter and more crowded. On the whole the marine form of the species appears to be constantly in a better state of nutrition than the fresh-water form. As the measurements given here indicate, the strobila is much wider and thicker and the scolex much larger; but what attracts one's attention at first sight is the clear-cut nature of the scolex and segments of this, the *proboscideus* type, which led Bellingham (1844:252) to describe it as "a very beautiful species," as compared to the other form. In the latter the posterior, much-crowded proglottides, especially, are often irregularly swollen transversely or longitudinally so as to present appearances in many cases quite like those to be seen in *A. rugosum*. Much of this may, however, be due to osmotic action when the worms are near the point of death with the possible low resistance of the body-wall of the posterior segments when growth and development have gone on to such a stage that they are little more than sacs filled with eggs. As pointed out by various writers the posterior borders of the segments are provided in the median line and on both surfaces with a distinct notch or emargination, which together form a longitudinal groove on each face of the chain. This is quite pronounced in the strobilas from the salmon but often not so marked in those from the whitefish, lake trout and ling. In these it is confined more to the posterior stretches of the segments and greatly exaggerated by the above mentioned irregular swellings which, however, do not cross the longitudinal groove formed by these notches. Often this groove may be present in the segments close to the scolex and again in posterior ones but absent in the middle stretches, where, of course, the emarginations are either almost absent or all but obliterated by the degree of relaxation. On the contrary, Olsson (1893:17) often found the groove only in the middle portions of the *infundibuliformis* form. Many specimens also show the condition described by Leuckart (1819:42) when he said, "Die hinteren Ränder dieser Glieder scheinen allerdings etwas verdickt und stehen an den Körperrändern sehr hervor." In the anterior segments of considerably relaxed or especially young strobilas something of the manner of segmentation can be seen. This was found to take place much as in the genus Bothriocephalus, altho the writer was not able to distinguish the primary segments to his satisfaction. What was considered to be such is shown in figure 64, a sketch of segments beginning 27mm. from the anterior end of the strobila in question. The idea of dominance of the anterior portions over the posterior portions in segmentation, as brought out under *B. scorpii*, is here shown very nicely. In the *proboscideus* type of strobila the same method of subdivision was followed in the anterior segments, altho with greater difficulty on account of the fact that the segments are so closely crowded in the longitudinal direction. Olsson (1867:53) noticed the subdivision of the segments producing an alternation of larger segments with smaller ones, and he considered it to be an *articulatio spuria* similar to that described by Wagener (1854:69) for *Amphicotyle heteropleura* and by Krabbe (1865:384) for *B. scorpii* and other species. Later Olsson (1893:17)

states that transverse divisions occured in *B. infundibuliformis* as well as in *B. proboscideus*. Finally, as regards the external features, it should be noted that the posteriormost, yet ripe proglottides of the smaller strobilas from the fresh-water hosts are quadrate in shape, often as long as broad, and usually somewhat narrower than the mature segments ahead. These, as stated by Olsson (1893:17), show practically nothing more in the way of reproductive organs than the lobed uterus-sacs. The following measurements of the scolex are given for the sake of comparison:

HOST	*Salmo salar*	*Cristivomer namaycush*		*Lota maculosa*
Length	1.01mm.	0.70mm.	0.87mm.	0.71mm.
Width of terminal disc	0.74	0.42	0.47	0.41
Width of bothrium (middle)	0.94	0.52	0.38	0.60
Length (laterally)	0.88	0.70	0.74	0.64
Depth of terminal disc	0.56	0.33	0.44	0.36
Depth posteriorly	1.25	0.40	0.55	0.68

The anatomy of the species was studied by Matz (1892:110), later writers referring to his work, altho Zschokke (1884:24), Lönnberg (1889:35) and Olsson (1893:17) made some valuable contributions, while Lühe (1899a and 1900a) dealt with it from a comparative standpoint. Most of them, however, confined their attention almost entirely to the reproductive organs.

The cuticula, from 4 to 5μ in thickness, is divisible into two layers besides the basement membrane, an outer and darker occupying about one-third of the thickness of the whole, and quite smooth, and an inner, quite light layer. It is slightly modified on the posterior borders of the segments to form minute spinelets which are evidently formed by the splitting of the somewhat thickened outer layer. This modification is, however, not so well marked as in other species. The subcuticula, from 60 to 100μ in thickness, extends from the cuticula to the longitudinal muscles, thus occupying the outer one-half of the cortex. Its nuclei are confined to its inner half, thus leaving the outer ends of the cells free. The whole tissue requires good fixation and preservation to show these features which in the older proglottides and longer strobilas are otherwise affected by the general degeneration coincident with the development of the enormous number of eggs produced by this species. And it should be stated here that this is more applicable to the large marine form than to those from fresh-water hosts. So far as the writer is aware no calcareous bodies have been described for this species. They were found only in the smallest strobilas with a maximum diameter of 15μ. The parenchyma is in the form of a very fine reticulum, the spaces of which form the bulk of the tissue.

Unlike *A. rugosum* the longitudinal muscles of the parenchyma are not arranged in fasicles; nor do the transverse fibres form a septum between even the anterior segments. The latter are often more numerous towards the posterior end of the segments, as are the sagittal fibres, but they do not prevent

the testes from being continuous from proglottis to proglottis, nor the anterior end of the uterus-sac from protruding considerably into the proglottis immediately ahead. In the material from *Lota maculosa* the myoblastic nuclei and protoplasm of the sagittal fibres are almost as prominent as in *A. rugosum*. There is a weakly-developed series of external longitudinal muscles arranged in relation to the posterior borders of the anterior segments as described above. The musculature of the ordinary form of the scolex is typical. Transverse or circular, sagittal or radial, and longitudinal muscles are about equally developed, the latter entering the base of the organ in scattered groups, altho not distinctly fascicled, and extending to the tip. A series of well developed longitudinally arcuate fibres, arranged around the border of the terminal disc is present, quite as described by the writer elsewhere (1914a:92) for *Haplobothrium globuliforme*. In the enlarged scolex from *L. maculosa*, altho the general arrangement of the musculature is retained, the number of fibres is greatly diminished and the whole ensemble indicative of not a little degeneration. This is emphasized by the fact that in the unenlarged portion of the organ there is to be seen in sections a deposition of material which stains much like that described above for the young pseudoscolices of *A. rugosum*. This is absent, however, from the enlarged terminal portion.

In the form from the salmon the chief nerve strands reach a maximum dorsoventral diameter of about 100μ by a transverse diameter of 40μ. They are located at the extreme lateral limits of the medulla, all of the testes coming between them, as pointed out by Lühe (1900a), and pass dorsal to the inner end of the cirrus-sac and consequently to the vagina, as mentioned by Matz (1892:112). In the scolex the chief strands enlarge at the level of the border of the terminal disc to form two ganglia which are united by a small transverse commissure, the whole arrangement being quite comparable to that present in *B. cuspidatus*.

Zschokke (1884:25) said that "Les canaux excréteurs sont parallèles et voisin des bords lateraux," while Fraipont (1881:12) described the system as follows: "La vesicule terminale est petite. Le système des *canaux descendants* est fort compliqué; ils fournissent des branches latérales de volume très variable; les unes volumineuses, les autres excessivement grêles. Les branches forment un réseau à mailles très inégales. Des canaux très fins peuvent partir directement des gros troncs. Dans la tête, les canaux descendants forment un reticulum très compliqué. Cretaines ramifications très fines se terminent par des entonnoirs ciliés identiques à ceux du *B. punctatus*." In mature proglottides about six of these descending canals are seen on each surface of the strobila, as stated by Matz, those on the ventral surface, altho of varying size, being constantly the largest. The outermost of these passes ventral to the cirrus-sac, while the corresponding dorsal one is much more median in position. All of the vessels lie just within or sometimes among the inner transverse muscles but not so much among the vitelline follicles as Matz found. In the first segments these twelve canals become reduced to three or four, irregularly arranged on each side of the median sagittal plane, of which one or two may

course outside of the nerve strand for considerable stretches. Only one large vessel, just within the nerve strand, passes into the base of the scolex on each side. These two are quickly reduced in size and disappear at about the middle of the scolex. In the youngest plerocercoids, such as shown in figure 50, there was seen at the posterior end a cuticular sac or invagination about 45μ in length by 10μ in diameter, much resembling an excretory vesicle. But since no vessels connected with this structure as in *A. rugosum*, its nature was not satisfactorily determined. On the other hand, the vessels of a young strobila which had evidently just lost some segments did not open on the concave posterior end but were lost in the parenchyma some distance from the end after considerable anastomosing.

The earliest traces of the reproductive rudiments appear in the marine type about 45mm. from the tip of the scolex while the first eggs are to be seen in the uterus 63mm. from the same point. The same data for a considerably relaxed strobila from *Coregonus clupeiformis* are respectively 62 and 225mm. Olsson (1893:17) found the first testes to appear in a 200mm. strobila from *Salmo alpinus* 95mm. from the anterior end, while 20mm. farther the uteri began to show. Depending a great deal on the amount of relative contraction of the proglottides, the genital cloaca is situated from one-third to half way along the margin of the segment, altho Matz (1892:112) stated that its location was between the first and second thirds of the edge of the proglottis. He also said that they (? the cirrus-sacs) always opened on the left margin of the strobila; but Lühe (1899) corrected this error by stating that altho they are situated on one side for long stretches, in reality they alternate from side to side. The writer also found them to be irregularly alternating but unilateral thru many proglottides. In one strobila from a whitefish, for instance, they were found to be arranged as follows, the numbers representing the numbers of proglottides in which they are on the same side before changing to the opposite margin: 16, 3, 2, 5, 41, 21, 19, 7, 7, 8, 13, 3, 4, 11, 28, 9, 7, 9, 35, 10, 26, 9, 7, 9, 35, 11; while in a stretch of gravid proglottides from *Cristivomer namaycush*, the lake trout, the data are: 27, 2, 80, 4, 3, 2, 13, beyond which the cirrus-sacs had so degenerated that it was found impossible to follow them with satisfaction in the toto preparations. Zschokke (1884:25) erroneously described the cirrus-pouch as being ". . . située vers le milieu de la face ventrale de chaque proglottis," while "L' orifice femelle se trouve en dessous, vers le bord postérieur du proglottis," thus leading Lönnberg (1889:35) to establish the new species *B. suecicus* which Matz (1892:111) considered with obvious justification to be synonymous with his *B. infundibuliformis*, or *A. crassum* as it is now known. The cloaca itself is tubular, from 50 to 60μ in depth in the fresh-water from and about 175μ in the marine form. In either case there is no sharply separated hermaphroditic duct, the cirrus and vagina opening very close together at the bottom of the pore, the latter constantly ahead of and more or less ventral to the former.

Matz stated that the testes were about 300 in number, 72μ in size, and extended from the median line to the lateral nerves, while Lühe (1900a) described

them as being between the uterus and the marginal nerves as in *B. imbricatus*. In the present study they were found to pass to the median line and dorsal to the uterus-sac in the anterior portion of the proglottis but to be prevented from doing so posteriorly by the ovary and the ducts in its immediate neighborhood. They are not all in the same horizontal plane but arranged in two or three pseudostrata (Fig. 92). Their number is from 40 to 150 in each proglottis with an average of 90, and their dimensions from 95 to 115μ in depth by 70 to 100 in transverse diameter, being roughly circular in frontal sections. The vas deferens forms an elongated mass of coils of quite the same shape and arrangement with the fewer coils before entering the cirrus-sac as in *A. rugosum*. Its dimensions are 0.35 to 0.60 by 0.15 to 0.18mm. In the proximal one-third to one-half of the cirrus-sac the male duct forms a mass of coils, the ejaculatory duct, which may or may not become enlarged with sperms to form at least a temporary inner seminal vesicle, while in the distal half of the pouch it continues in an almost straight course as the cirrus proper with a maximum diameter of 20μ. The cirrus-sac varies in dimensions from 130 to 220 by 60 to 105μ in the fresh-water form and 255 to 380 by 120 to 150μ in the form from *Salmo salar*, and is ovoid in shape with the smaller end, often quite pointed, towards the genital cloaca. Matz gave the length of the cirrus-sac as 255μ for the form from the European salmon and salmon trout. The wall is comparatively thinner and there are fewer parenchymatous nuclei around it or within it among the conspicuous retractor muscles than in *A. rugosum*.

The vagina opens constantly ahead of the cirrus and more or less ventral to it as pointed out by Matz (p. 112). From this point it bends backward and gradually downward, thus making a bow which lies below the coils of the vas deferens, and then courses mediad parallel to the anteroventral border of the latter. Near the median line, however, it again rises to pass over the lateral border of the ovary before gaining the oviduct. There is thus a broad ventral bow to the vagina, which, contrary to Lühe's statement, is more median than in *A. rugosum*. Opposite the cirrus-sac the vagina may be found enlarged to a diameter of 35μ. The ovary is quite irregular or only very roughly kidney-shaped as stated by Lühe (1900a), and has a maximum diameter in the marine form of 0.8mm. by a length of 0.13mm. As in *A. rugosum*, there is a very broad isthmus, with the posterodorsal part of which the oviduct is connected by the oocapt which has a diameter of 40μ. The oviduct receives the vagina in the median coronal plane. Usually two small vitelline ducts passing along the ventral floor of the medulla unite in the median line to form a common duct which is not enlarged to form a reservoir; but in the material from Lota two others were seen to unite dorsally to form another common duct, while the ventral duct formed a number of anastomoses with its tributaries before uniting with the oviduct. Matz described the vitelline follicles as irregular in shape, discontinuous from proglottis to proglottis and located among the longitudinal muscles, there being about 29 "on the surface," presumably in transverse sections. The writer likewise found them to be quite irregular in shape and to range in location from among the inner longitudinal muscles to distinctly out-

side of them and even among the subcuticular nuclei in the *proboscideus* form. In toto mounts of anterior segments they may be seen to be quite discontinuous and, as pointed out by Lühe (1900a), arranged in two lateral fields on each surface, there being a few, however, in the median ventral line. The combined ootype and shell-gland is a small inconspicuous compact structure lying close to the dorsal wall of the medulla as in *A. rugosum*. The uterine duct also takes only a very few coils before expanding into the capacious uterus-sac. Matz described the latter as being not round as in *B. scorpii* and *B. claviceps*, but pointed towards each side, which points do not disappear when the sac is filled with eggs, while Lühe (1910:17) repeats this statement. In the material studied by the writer only the young uterus-sacs, much elongated in the transverse direction, were found to be pointed laterally, but the mature structures, i.e., when filled with eggs, distinctly rounded or only very broadly pointed in some cases (Fig. 77). In dorosoventral view the sac varies in shape from an elliptical or quadrate, lobed organ, filling up most of the proglottis in the fresh-water form, to a transversely much elongated cavity in the *proboscideus* form, so enlarged in mature joints that the strobila in such gravid regions is little else than a tube filled with eggs. The openings are situated in the median line on the ventral surface, each one being just opposite the posterior emargination of the segment immediately ahead.

Matz states that the egg measures 54.5 by 40.9μ, but the writer found them of quite different sizes when removed from gravid segments in the 5% formalin solution in which they were preserved. In general, two sizes were seen, small ones with thicker darker shells and larger ones with thinner lighter shells, but at the same time all intermediate sizes between these forms. Those from the fresh-water form of the species measured 55 to 115 by 35 to 75μ, while those from the form from *Salmo salar* were 45 to 110, by 30 to 75μ, thus showing that so far as the size of the eggs goes, at least these two forms are one and the same species.

So far as the writer is aware the development of the egg of this species has been studied only by Koelliker (1843:91) and later by Braun (1889:668, etc.) in review. Several writers have described various young plerocercoids. The youngest found by Olsson (1867:53) was only 2mm. in length and had only three segments, a neck and several longitudinal spiral excretory canals, of which two extended to the anterior part of the head. The triangular caudal piece of this young strobila had a median sinus posteriorly, thus indicating, perhaps, in the light of the present contributions, that a portion had already diasppeared. Leuckart (1878:605) spoke of the simplicity of the development of the plerocercoid, while Zschokke (1884:27) believed that he had found the larvae of *B. infundibuliformis* in numerous cysts on the outside of the walls of the alimentary tract of *Perca fluviatilis*, *Trutta vulgaris*, *Esox lucius*, *Salmo umbla*, *Thymallus vulgaris* and *Lota vulgaris*. They were also found on the liver, the spleen, the ovaries and the peritoneum of the same fishes, with their scolices ordinarily invaginated and with lengths of from 2 to 6mm. In 1893 Olsson again referred to the plerocercoids and younger strobilas. In *Lota vul-*

garis he found young strobilas, still possessing the rounded caudal piece but no neck, with the habit of invaginating their scolices. In a *Salmo salar* he found on July 4th similar young "scolices" (plerocercoids) not only free in large numbers in the intestine of the host posterior to the pyloric ceca but also present along with the anterior ends of adult strobilas in the ceca themselves. Again in June he found a great many young strobilas in *S. alpinus*. These facts, together with the further fact that the adult worms have been found in the hosts during every month of the year, points to infection of the final host with the pleroceroids at all times of the year. Of chief interest in this connection is the finding by Schneider (1902:28) of young plerocercoids 2 to 7mm. long free in the stomach and intestine of *Clupea harengus membras* L., which he believed to be the young stages of *Bothriotaenia proboscidea* (Batsch), as he called the species. They were found in greater numbers towards the latter part of June than at other times during the summer. Concerning the significance of the location of the larvae in these herring, he said: "Daher muss ich annehmen, dass dieser Fisch nicht der erste, sondern der zweite Zwischenwirth des Bandwurmes ist. Erster Zwischenwirth, in welchem der Wurm sein Cystenstadium durchläuft, muss wohl ein Arthropode (Kruster oder Insectenlarve) sein, der dem Ostseeheringe sehr oft zur Nahrung dient. Falls meine Annahme richtig ist, woran ich nicht zweifele, das *Clupea harengus membras* L. derjenige Zwischenwirth ist, mit dem der Ostseelachs direct die Larven von *B. proboscidea* in seinen Darmkanal aufnimmt, so erklärt sich leicht das Zustandekommen solcher Wasserinfectionen, wie sie an den Ostseelachsen beobachtet werden." Lühe (1910:12) briefly reviewed the findings of these bothriocephalid larvae in various hosts up to date and pointed out that those of *Diphyllobothrium latum* have often been confused with those of *A. crassum* and that in many cases it is doubtful whether either was certainly at hand. Ward (1910:1184) reported the species from *Salmo salar sebago* and *Cristovomer namaycush*, but was unable to throw any light on the life-history altho he investigated the Sebago smelt as the possible intermediate host. No larvae were found in the latter, but concerning the infection of the final host, he said: "This is worthy of note that all of these parasites were full grown; not a single specimen was found which was not discharging ripe proglottides. Consequently the infestation must have taken place somewhat earlier in the year." The youngest lots of material studied by the writer were two taken from *Lota maculosa* from Lake Ontario, off Port Credit, near Toronto, on Nov. 5 and 8, 1912, and one from the intestine of a young *Cristovomer namaycush* from the same locality on the latter date. The lot from the lake trout contained all stages from that shown in figure 50 to the largest which by comparison with adult specimens from the same host were found to belong to this species. While no stages were found between that shown in figure 52 and that shown in figure 50 altho two others were only very slightly larger than the latter, it seems reasonable to consider the latter itself to belong to this series and to represent the earliest stage of the same. Figures 53 and 54, two later stages, are given to show the manner of beginning of the segmentation and the early

dropping off of two or more very immature segments from the hinder end. The first indication of this is probably represented in figure 52, altho the strobila in figure 53 does not show it. The relative ages, however, of these two is difficult to state definitely since the first one is more contracted longitudinally than the other. On the other hand, two intermediate in length between those shown in figures 53 and 54, were indented posteriorly, thus showing that some of the earliest segments had already been lost. Thus it is seen that at a very early period in the development of the strobila of this species there are lost a few of the first-formed segments in much the same way as the bladder of the cysticercus of the taenioid cestodes is cast off in the final host.

The material studied consisted of lots 86, 87, 88, 303 and 304 from *Salmo salar*, 38a, b, c, d, e, and o, 66, 67, 164, 167 and 192 from *Cristivomer namaycush*, 42 and 166 from *Coregonus clupeiformis*, and 61, 62, 381, and 387 from *Lota maculosa*, in the writer's collection; Ch 26a, Ch 26b, Ch 29a, Ch 29b, Ch34a, T1g, T2q and 17.186 from *C namaycush*, and Ch 13b and Ch 22b from *Lota maculosa*, in the collection of the University of Illinois; and 509c, 511a, 520b, 524a, 525a and 530a from *Salvelinus fontinalis*, 613b and 622d from *Lota maculosa* and 616-620c from "whitefish," in the collection of Dr. G. R. LaRue.

BIBLIOGRAPHY

*Abildgaard, P. C.
1790. Almindelige Betragtninger over Indvolde-Orme, Bemaerkninger ved Hundsteilens Baendelorm, og Beskrivelse med Figurer af nogle nye Baendelorme. Skr. Naturh. Selsk., V, 1:26-64.

Ariola, V.
1896. Sopra alcuni Dibotrii nuovi o poco noti e sulla classificazione del gen. Bothriocephalus. Atti soc. ligust. sc. nat. geogr. Genova, 7:261-82, pl. 4.
1896a. Sulla Bothriotaenia plicata Rud. e sul suo sviluppo. Nota. Atti soc. ligust. sc. nat. geogr. Genova, 7:117-26.
1900. Rivisione della famiglia Bothriocephalidae, s. str. Arch. parasitol., 3:369–484, pl. 8-10.

Baird, W.
1853. Catalogue of the species of entozoa, or intestinal worms, contained in the collection of the British Museum. 133 pp., 2 pl. London.

Barbagallo, P. and Drago, U.
1903. Primo contributo allo studio della fauna elmintologica dei pesci della Sicilia orientale. Arch. parasitol., 7:408–27.

Batsch, A. J. G.
1786. Naturgeschichte der Bandwurmgattung überhaupt und ihrer Arten insbesondere, nach den neuern Beobachtungen in einem systematischen Auszuge. 298 pp., 6 pl. Halle.

Bellingham, O'Bryan
1844. Catalogue of Irish Entozoa, with observations. Ann. mag. nat. hist., 13:101-105, 167-74, 254-60, 335-40, 422-30; 14:162-65, 251-56, 317-23, 396-403.

Benham, W. B.
1901. A Treatise on Zoology; E. R. Lankester. Part IV. The Platyhelmia, Mesozoa and Nemertini. 204 pp. London.

Blanchard, R.
1894. Notices sur les parasites de l'homme (troisième série), 4. Sur le *Krabbea grandis*, et remarques sur la classification de bothriocephalines. C. R. soc. biol. Paris, 46:699–702.

Bloch, M. E.
*1779. Beitrag zur Naturgeschichte der Würmer, welche in anderen Thieren leben. Beschft. Berl. Gesellsch. naturf. Fr., 4:534–61, pl. 12, 14–15.
1782. Abhandlung von der Erzeugung der Eingeweidewürmer und den Mitteln wider dieselben. 54 pp., 10 pls. Berlin.

*Bosc, L. A. G.
1802. Histoire naturelle des vers. 3 vols. Paris.

Braun, M.
1891. Helminthologische Mittheilungen. Centrbl. Bakt. Parasit., 9:52–56.
1894–1900. Vermes: Cestodes. Bronn's Klassen und Ordnungen des Thierreichs, 4, Abt. 1, b.

*Briganti, V.
1819. Descrizione delle ligule, che abitano nell' addomine de ciprini del lago di Palo in prov. di principato Citra. Atti acad. sc. Napoli, cl. fis. stor. nat., 1:209–33.

*Items starred were not consulted in the original

CARUS, J. V.
1885. Vermes. Prodromus faunae Mediterraneae, 1:112–282. Stuttgart.

CARUS, J. V. and GERSTAECKER, A.
1863. Handbuch der Zoologie, 2 vols. Leipzig.

COBBOLD, T. S.
1858. Observations on Entozoa. Trans. Linn. Soc. London, 22:155-72, pl. 31-33.
1879. Parasites; a treatise on the Entozoa of man and animals, including some account of the Ectozoa. 519 pp., 85 figs. London.

COHN, L.
1898. Untersuchungen über das centrale Nervensystem der Cestoden. Zool. Jahrb., Anat., 12:89–160, pl. 6–9.
1902. Zur Kenntnis des Genus Wagneria Monticelli und anderen Cestoden. Centrbl. Bakt. Parasit., Abt. 1, 33:53–60.

COOPER, A. R.
1914. On the Systematic Position of *Haplobothrium globuliforme* Cooper. Trans. Roy. Soc. Can., (3)8, sec. 4, p. 1–5.
1914a. A New Cestode from *Amia calva* L. Trans. Roy. Can. Inst., 10:81–119, pl. V-VII.
1917. A Morphological Study of Bothriocephalid Cestodes from Fishes. Journ. Parasit., 4:33–39, 2 pl.

CREPLIN, F. C. H.
1839. Eingeweidewürmer, Binnenwürmer, Thierwürmer. Allg. Encycl. Wiss. Künste (Ersch. u. Gruber), Sect. 1, 32:277–302. Leipzig.

DIESING, C. M.
1850. Systema helminthum, 1, 692 pp. Vindobonae.
1854. Ueber eine naturgemässe Verteilung der Cephalocotyleen. Sitzsber. Kais. Akad. Wiss., math.-naturw. Cl., 13:556–616.
1863. Revision der Cephalocotyleen, Abth. Paramecocotyleen. Sitzsber. Kais. Akad. Wiss., math.-naturw. Cl., 48:200–345.

DONNADIEU, A. L.
1877. Contribution à l'histoire de la ligule. Journ. anat. physiol., 13:321-70, pl. 14-20.

DRUMMOND, J. L.
1838. Notices of Irish Entozoa. Mag. Nat. Hist., n.s., 2:515–24, 571-77, 655-62.

*DUCHAMP, G.
1876. Recherches anatomiques et physiologiques sur les ligules. Jour. Zool., 5:372–73.

DUJARDIN, F.
1845. Histoire naturelle des helminthes ou vers intestinaux. 685 pp., 12 pl. Paris.

DUVERNOY, G. L.
1842. Note sur un nouveau genre de ver intestinal, de la famille des ténioides, le bothrimone de l'esturgeon (*Bothrimonus sturionis*, Nob.) p. Ann. sci. nat., zool., (2) 18:123–26, pl. 3B.

*ESCHRICHT, D. F.
1841. Anatomisch-physiologische Untersuchungen über die Bothryocephalen. Nova acta acad. nat. curios., 19, suppl. 2, 161 pp., 3 pl.

FABRICIUS, O.
1780. Fauna groelandica, systematice sistens animalia Groelandiae occidentalis hactenus indagata. 470 pp., 1 pl. Hafniae et Lipsiae.

FRAIPONT, J.
1880. Recherches sur l'appareil excréteur des trematodes et des cestodes, 2e communication; 3e communication. Bull. acad. roy. Belg., 50:106–7, 265-70.
1881. Recherches sur l'appareil excréteur des trematodes et des cestodes; deuxième partie. Arch. biol., 2:1–40, pl. 1-2.

FUHRMANN, O.
1896. *Bothriocephalus zschokkei* nova species. (Beitrag zur Kenntnis der Bothriocephalen.) Centrbl. Bakt. Parasit., Abt. 1, 19:546–50.
1898. Ist *Bothriocephalus zschokkei* mihi synonym mit *Schistocephalus nodosus* Rud.? Zool. Anz., 21:143-45.
1902. Sur un nouveau Bothriocephalide d'oisseau (*Ptychobothrium armatum*). Arch. parasit., 5:440–48.
1910. *Triaenophorus robustus* Olsson dans les lacs Neuchâtel et de Bienne. Bull. soc. sc. nat. Neuchâtel, 36:86–89.

GAMBLE, F. W.
1896. Platyhelminthes and Mesozoa. Cambridge Natural History, 2; 96 pp., 47 ill. London.

GEMMILL, J. F.
1909. A Specimen of *Ligula simplicissima*, Rudolphi; with Notes on the Life-History of the Ligulinae. Glasgow Naturalist, 2:6–12.

GMELIN, J. F.
1790. Caroli a Linne . . . Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis, 1:3021–3910. Lipsiae.

GOEZE, J. A. E.
1782. Versuch einer Naturgeschichte der Eingeweiderwürmer thierischer Körper, 480 pp., 44(35) pl. Blankenburg.

GRIMM, O.
1871. Zur Anatomie der Binnenwürmer. Zeit. wiss. Zool., 21:499–504.

HOFER, B.
1904. Handbuch der Fischkrankheiten. Stuttgart, 1906.

HUNTSMAN, A. G.
1915. Fresh-Water Malacostraca of Ontario. Contrib. Can. Biol., Fasc. II, Suppl., 47th Ann. Rep. Dep. Mar. Fisheries. Ottawa, Canada.

JANICKI, C. V.
1906. Studien an Säugethiercestoden. Zeit. wiss. Zool., 81:505–97, 6 pl.

JOHNSTONE, J.
1907. Internal Parasites and Diseased Conditions of Fishes. Trans. Biol. Soc. Liverpool, 21:170–203.
1909. Internal Parasites and Diseased Conditions of Fishes. Trans. Biol. Soc. Liverpool, 32:87–100.

KESSLER, K. T.
*1868. Beiträge zur zoologischen Kenntnis des Onegasees und dessen Umgebung. Beil. Arb. russ. naturf. Vers. Petersburg, 1868, 183 pp., 8 pl. [Russian text.]

KIESSLING, F.
1882. Ueber den Bau von *Schistocephalus dimorphus* Creplin und *Ligula simplicissima* Rudolphi. Arch. Naturg., 1:241-80, pl. 14–15.

KOELLIKER, R. A. VON
1843. Beiträge zur Entwickelunggeschichte wirbelloser Thiere. Arch. Anat., Physiol., wissensch. Med., p. 68–141, pl. 6–7.

KRABBE, H.
1865. Helminthologiske Undersøgelser i Danmark og paa Island, med saerligt Hensyn til Blæreormlidelserne paa Island. K. Danske vidensk. selsk. skr., naturv. math. Afd., (5) 7:347–408, pl. 1–7.
1874. Diplocotyle Olrikii, cestoide non articulé du groupe des bothriocéphales. Jour. Zool. 3:392–5, 1 pl.

KRAEMER, A.
1892. Beiträge zur Anatomie und Histologie der Cestoden der Süsswasserfische. Zeit. wiss. Zool., 53:647–722, Taf. XXVII–XXVIII.

LAMARCK, J.
1816. Histoire naturelle des animaux sans vertèbres. Vol. 3, 586 pp. Paris.

LANG, A.
1881. Untersuchungen zur vergleichenden Anatomie und Histologie des Nervensystems der Plathelminthen. III. Das Nervensystem der Cestoden in Allgemeinen, dasjenige der Tetrarhynchen in Besonderen. Mitth. zool. Stat. Neapel, 2:372–400, pl. 15–16.

LEIDY, J.
1855. Notices of some tapeworms. Proc. Acad. Nat. Sci. Philad., 7:443.
1856. A synopsis of entozoa and some of their ectocongeners observed by the author. Proc. Acad. Nat. Sci. Philad., 8:42-58.

LEUCKART, F. S.
1819. Zoologische Bruchstücke: Das Genus Bothricephalus Rud. 70 pp., 2 pl. Helmstadt.

LEUCKART, R.
1878. Archigetes Sieboldi, eine geschlechtsreife Cestodenamme. Zeit. wiss. Zool., Suppl. 30:593-606.

LINNAEUS, C.
1758. Systema naturae. Ed. X, Holmiae.
1767. Systema naturae. Ed. XII, Holmiae.

LINSTOW, O. VON
1878. Compendium der Helminthologie. 404 pp. Hannover.
1889. Helminthologisches. Arch. Naturg., 1:235–46, pl. 16.
1901. Entozoa des zoologischen Museum der kaiserlichen Akademie der Wissenschaften zu St. Petersburg. Bull. acad. Imp. sci. St. Petersburg, (V) 15:271–92.
1901a. Die systematische Stellung von *Ligula intestinalis* Goeze. Zool. Anz., 24:627–34
1903. Entozoa des zoologischen Museums der kaiserlichen Akademie der Wissenschaften zu St. Petersburg, 2. Ann. mus. zool. acad. Imp. sci. St. Petersburg, 8:265-94 pl. 17-19.
1904. Beobachtungen an Nematoden und Cestoden, Arch. Naturg., 1:297–309, pl. 13.

LINTON, E.
1889. Notes on entozoa of marine fishes of New England with descriptions of several new species. Ann. Rep. U. S. Comm. Fish and Fisheries, 14:453–511.
1890. Notes on entozoa of marine fishes of New England with descriptions of several new species. Ann. Rep. U. S. Comm. Fish and Fisheries, 15:719–899.
1891. On two Species of larval Dibothria from the Yellowstone National Park. Bull. U. S. Fish Comm., 9:65–79, pl. 23–27.

1897. Notes on larval cestode parasites of fishes. Proc. U. S. Nat. Mus., 19:787–824.
1898. Notes on cestode parasites of fishes. Proc. U. S. Nat. Mus., 20:423–56, pl. 27–34.
1901. Fish parasites collected at Woods Hole in 1898. Bull. U. S. Fish Comm., 19:267–304.
1901a. Parasites of fishes of the Woods Hole region. Bull. U. S. Fish Comm., 19:405–92.

LÖNNBERG, E.
1889. Bidrag till Kännedomen om i Sverige förekommande Cestoder. Bihang K. Svenska Vet. Akad. Handl., 14:1–69.
1890. Helminthologische Beobachtungen von der Westküste Norwegens. Bihang K. Svenska Vet. Akad. Handl., 16:1–47.
1891. Anatomische Studien über skandinavischen Cestoden. Kgl. Svensk. Vet. Akad. Handl., 24:1–109, 3 pl.
1893. Bemerkung über einige Cestoden. Bihang K. Svensk. Vet. Akad. Handl., 18, 17 pp., 1 pl.
1897. Beiträge zur Phylogenie der parasitischen Plathelminthen. Centrbl. Bakt. Parasit., Abt. 1, 21:674–84.

LÜHE, M.
1896. Das Nervensystem von *Ligula* in seinem Beziehung zur Anordnung der Musculatur. Zool. Anz., 19:383–84.
1897. *Bothriocephalus zschokkei* Fuhrmann. Centrbl. Bakt. Parasit., Abt. 1, 22:586.
1897a. Die Anordnung der Musculatur bei den Dibothrien. Centrbl. Bakt. Parasit., Abt. 1, 22:739–47.
1897b. *Bothriocephalus zschokkei* Fuhrmann. Zool. Anz., 20:430–34.
1898. Die Gliederung von *Ligula*. Centrbl. Bakt. Parasit., Abt. 1, 23:280–86.
1899. Zur Anatomie und Systematik der Bothriocephalen. Verhandl. deutsch. zool. Gesellsch., Leipzig, 30–55.
1899a. Beiträge zur Kenntnis der Bothriocephalen. I. Bothriocephalen mit marginalen Genitalöffnungen. Centrbl. Bakt. Parasit., Abt. 1, 26:702–19.
1900. Ueber *Bothrimonus* Duv. und verwandte Bothriocephalen. Zool. Anz., 23:8–14.
1900a. Untersuchungen über die Bothriocephalen mit marginalen Genitalöffnungen. Zeit. wiss. Zool., 68:43–112, pl. 4–7.
1900b. Die Bothriocephalen der landbewohnenden Reptilien. Centrbl. Bakt. Parasit., Abt. 1, 27:209–17, 252–58.
1901. Ariola, V. Rivisione della famiglia Bothriocephalidae, s.str. Centrbl. Bakt. Parasit., 29:412–16.
1902. *Urogonoporus armatus*, ein eigentumlicher Cestode aus *Acanthias*. Arch. Parasit., 5:209–50.
1902a. Revision meines Bothriocephalidensystemes. Centrbl. Bakt. Parasit., Abt. 1, 31:318–31.
1902b. Bemerkungen über die Cestoden aus *Centrolophus pompilius*. I. Zur Synonymie der *Centrolophus*-Cestoden. Centrbl. Bakt. Parasit., Abt. 1, 31:629–37.
1910. Parasitische Plattwürmer. II: Cestodes. Die Süsswasserfauna Deutschlands, Brauer, Heft 18, 153 pp.

LUTHER, A.
1909. Ueber *Triaenophorus robustus* Olsson und *Henneguya zschokkei* Gurley als Parasiten von *Coregonus albula* aus dem See Sapsojärvi. Medd. soc. fauna flora fenn., 35:58.

MATZ, F.
1892. Beiträge zur Kenntnis der Bothriocephalen. Arch. Naturg., 58:97–122, pl. 8.

MINCKERT, W.
1905. Ueber Epithelverhältnisse und Strucktur der Körpercuticula. Zool. Anz., 29: 401–8.

MOLIN, R.
1858. Prospectus helminthum, quae in prodromus faunae helminthologicae Venetiae continentur. Sitzber. Kais. Akad. Wiss., math.-naturw. Cl., 30:127–58.
1861. Prodromus faunae helminthologicae venetae adjectis disquisitionibus anatomicis et criticis. Denkschr. Kais. Akad. Wiss., math.-naturw. Cl., 19:189–338.

MONIEZ, R.
1881. Mémoire sur les Cestodes. Trav. inst. zool. Lille, 3; 238 pp., 12 pl.

MONTICELLI, F. S.
1890. Note elmintologiche. Boll. soc. nat. Napoli, (1) 4:189–208, pl. 8.
1892. Sul genere *Bothrimonus* Duv. e proposte per una classificazione dei Cestodi. Monit. zool. ital., 3:49–53.

MÜHLING, P.
1898. Die Helminth-Fauna der Wirbelthiere Ostpreussens. Arch. Naturg., 1:1-118, 4 pl.

MÜLLER, O. F.
1776. Zoologicae Danicae prodromus, seu animalium Daniae et Norvegiae indigenarum characteres, nomina, et synonyma imprimis popularium. 309 pp. Havniae.
*1780. Von Bandwürmern. Naturforscher, Halle, 14:129-203.
1788. Zoologica Danica seu animalium Daniae et Norwegiae rariorum ac minus notorum descriptiones et historia. 2, 56 pp., 39 pl. Havniae.

NEVEU-LEMAIRE, M.
1909. Sur la présence d'une larve de ligule (*Ligula simplicissima*) dans la cavité cranienne d'une tanche (*Tinca vulgaris*) C. R. soc. biol. Paris, 66:88.

NICOLL, W.
1907. A contribution towards a knowledge of the entozoa of British marine fishes. Part I. Ann. mag. nat. hist., (7)19:66-94, 4 pl.
1910. On the entozoa of fishes from the Firth of Clyde. Parasit., 3:322–59, pl. 19.

NIEMIEC, J.
1888. Untersuchungen über das Nervensystem der Cestoden. Arb. zool.-zoot. Inst. Univ. Wien, 7:1–60, 2 Taf.

NITZSCH, C. L.
1824. *Bothriocephalus*; *Brachionus*. Allg. Encyc. wiss. Kunste (Ersch u. Gruber), 12:94–99.

OLSSON, P.
1867. Entozoa, iakttagna hos skandinaviska hafsfiskar. I. Platyhelminthes. Lunds Univ. Arsskr., math. naturv.-vet., 3, 59 pp., pl. 1, 2.
1872. Om *Sarcotaces* och *Acrobothrium*, två nya parasitslägten fran fiskar. Oefvers. K. Svensk. vet.-acad. Förhdl., 29:37–44, 1 Taf.
1876. Bidrag till kännedomen om Jemtland's Fauna. Oefvers. K. Svensk. vet.-akad. Förhdl., 33:103–51.
1893. Bidrag till skandinaviens helminthfauna. 2. Handl. K. Svensk. vet.-akad., n. F. 25, 41 pp., 5 pl.

PALLAS, P. S.
1781. Bemerkungen über die Bandwürmer in Menschen und Thieren. Neue nord. Beytr. phys. geogr. Erd.-Völkerb., 1:39–112, 2 Taf.

PARONA, C.
1899. Catalogo di elminti raccolti in vertebrati dell'isola d'Elba dal Dott. Giacomo Damiani. Boll. mus. zool. Genova, No. 77, 16 pp.
1902. Catologo di elminti raccolti in vertebrati dell' isola d'Elba. Seconda nota. Atti. soc. lig. sci. nat. geogr. Genova, 13:10–29.

PARONA, C. and MAZZA.
1900. Sulla castrazione temporanea della Aterine dovuta ad elmintiasi. Atti soc. lig. sci. nat. geogr. Genova, 11:231–37.

PERRIER, E.
1878. Classification des cestoides. C. R. acad. sci. Paris, 86:552–54.
1897. Traité de zoologie. 2:1345–2136.

PILAT, A.
1906. *Bothriocephalus punctatus* bei Fischen. [Abstract by Udinsky in Zeit. Fleisch u. Milchhyg., 16:191.]

*PINTNER, T.
1880. Untersuchungen über den Bau des Bandwürmkörpers mit besonderen Berücksichtigung der Tetrabothrien und Tetrarhynchen. Arb. zool. Inst. Univ. Wien, 3:163–242, Taf. 14–18.

POLONIO, A. F.
1860. Catalogo dei cefalocotilei italiani e alcune osservazioni sul loro sviluppo. Atti soc. ital. sci. nat. Milano, 2:217–29, pl. 7.

QUEYRON, PH.
1905. La Ligulose chez les poissons d'eau douce dans le départment de la Gironde. Proc. verb. soc. Linn. Bordeaux, 60:CV–CVIII.

*RATKE, J.
1799. Iattagelser henhørende til Indvoldeormenes og Bløddyrenes Naturhistorie. Skr. naturh.-selsk., 5:61–148, pl. 2–3.

RIEHM, G.
1882. Fütterungsversuche mit *Ligula simplicissima*. Zeit. Naturw., 55:274–6, 328–30.

RIGGENBACH, E.
1896. Bemerkungen über das Genus *Bothriotaenia* Railliet. Centrbl. Bakt. Parasit., 20:222–31.
1898. *Cyathocephalus catenatus*. Zool. Anz., 21:639.

ROBOZ, Z. VON
1882. Beiträge zur Kenntnis der Cestoden. *Solenophorus megalocephalus*. Zeit. wiss. Zool., 37:263–85, 2 Taf.

RUDIN, E.
1914. Studien an *Fistulicola plicatus*. Rud. Rev. suisse zool., 22:321–63, 2 pl.

RUDOLPHI, C. A.
1793. Observationes circa vermes intestinales. Diss. in fasc. I praes. Jo. Quistorp. Fasc. II, praes. C. E. Weigel. Gryphswald.
*1801. Beobachtungen über die Eingeweidewürmer. Arch. Zool. Zoot., 2; 65 pp.
*1802. Fortsetzung der Beobachtungen über die Eingeweidewürmer. Arch. Zool. Zoot., 2; 67 pp.
1808. Entozoorum sive vermium intestinalium historia naturalis, 1. 579 pp., 6 pl. Amstelaedami.
1809. Entozoorum sive vermium intestinalium historia naturalis, 2(1). 457 pp., pl. 7–12. Amstelaedami.
1810. Entozoorum sive vermium intestinalium historia naturalis, 2(2). 398 pp. Amstelaedami.
1819. Entozoorum synopsis cui accedunt mantissa duplex et indices locupletissimi. 821 pp., 3 pl. Berolini.

SAINT-REMY, G.
1900. Contributions a l'étude du développment des Cestodes. I. Le développment embryonnaire dans le genre Anoplocephala. Arch. Parasit., 3:292–315.

SCHAEFER, R.
1913. Die Entwickelung der Geschlechtsausführwege bei einigen Cestoden mit besonderer Berücksichtigung der Epithelverhältnisse. Zool. Jahrb., Anat., 35:583–624.

SCHAUINSLAND, H.
1885. Die embryonale Entwickelung der Bothriocephalen. Jen. Zeit. Naturw., 19: 520–78.

SCHNEIDER, G.
1902. Über das Vorkommen von Larven des Bandwurms *Bothriotaenia proboscidea* Batsch im Magen und Darm von Ostseeheringen (*Clupea harengus membras* L.). Sitz.-ber. Ges. nat. Freunde, 1902:28–30.
1902a. Ichthyologische Beiträge III. Ueber die in Fischen des finnischen Meerbusens vorkommende Endoparasiten. Acta soc. fauna flora fenn., 22:1–87.
1903. Beiträge zur Kenntnis der Helminthfauna des finnischen Meerbusens. Acta soc. fauna flora fenn., 26:1–34, 1 pl.
1904. Ueber zwei Endoparasiten aus Fischen des finnischens Meerbusens. Medd. soc. fauna flora fenn., 29:75.

*SCHRANK, F. v. P.
1788. Verzeichniss der bisher hinlänglich bekannten Eingeweidewürmer, nebst einer Abhandlung über ihre Anverwandtschaften, 122 pp., 1 tab. München.

SCOTT, T.
1909. III. Some notes on fish parasites. Ann. Rep. Fish. Board Scotland, 26, pt. III, 73–92.

SHIPLEY, A. E.
1901. On a new species of *Bothriocephalus*. Proc. Camb. phil. soc., 11:209–13, 1 pl.

SOLOWIOW, P.
1911. Helminthologische Beobachtungen. Centrbl. Bakt. Parasit., Abt. 1, 60:93–132.

SPENGEL, J. W.
1905. Die Monozootie der Cestoden. Zeit. wiss. Zool., 82:252–87.

STEENSTRUP, J. J. S.
*1859. Beobachtungen und Bemerkungen über den Bandwurm des Stichlings, *Fasciola intestinalis* L., *Schistocephalus solidus* O. F. Müller, übers. v. Creplin Zeit. ges. Naturw., 14:475–85.

STILES, C. W. and HASSALL, A.
1894. A Preliminary Catalogue of the Parasites, contained in the Collections of the U. S. Bur. Anim. Ind., U.S. Army Med. Mus., Biol. Dept. Univ. Penn. (Coll. Leidy) and in Coll. Stiles and Coll. Hassall. Vet. Mag., 1:245–253; 331-354.
1902. Eleven papers on Animal Parasites. Bur. Anim. Ind., Bull. 35.
1912. Index Catalogue of Medical and Veterinary Zoology, Subjects: Cestodes and Cestodaria. Hyg. Lab. Bull. 85.

STOSSICH, M.
1890. Elminti veneti raccolti dal Dr. Alessandro Conte di Ninni. Boll. soc. adriat. sci. nat. Trieste, 12:49–56.
1891. Elminti veneti raccolti dal Dr. Alessandro Conte di Ninni, e descritti da Michaele Stossich. Boll. soc. adriat. sci. nat. Trieste, 13:1–8, 1 pl.
1898. Saggio di una fauna elmintologica di Trieste e provincie contermini. Prog. civ. scuola sup. Trieste, 162 pp.
1899. Appunti di elmintologica. Boll. soc. adriat. sci. nat. Trieste, 19:1–6, 1 pl.
1901. Osservazioni elmintologiche. Boll. soc. adriat. sci. nat. Trieste, 20:89–103.

SUMNER, F. B., OSBURN, R. C. and COLE, L. J.

1913. A Biological Survey of the Waters of Woods Hole and Vicinity. A Catalogue of the Marine Fauna. Bull. U. S. Bur. Fisheries, 31:549–794.

THOMPSON, W.

*1844. Additions to the Fauna of Ireland. Ann. mag. nat. hist., 13:430–40.

VAN BENEDEN, P. J.

*1849. Les helminthes cestoides. Bull. acad. roy. Belg., 16:269–82.

1850. Recherches sur la faune littorale de Belgique; les vers cestoides. Mém. acad. roy. Belg., 25, 119 pp., 24 pl.

1858. Mémoire sur les vers intestinaux. Compt. rend. acad. sci. Paris; (suppl.) 2:1–376, pl. 1–27.

1871. Les poissons des cotes de Belgique, leurs parasites et leurs commensaux. Mém. acad. roy. Belg., 38, 120 pp., pl. I–VI.

VOLZ, W.

1900. Beitrag zur Kenntnis einiger Vogelcestoden. Arch. Naturg., 1:115-174.

WAGENER, G. R.

1854. Die Entwickelung der Cestoden. Nova acta acad. nat. curios. (suppl.), 24:21–91, 12 pl.

1857. Beiträge zur Entwickelungsgeschichte der Eingeweidewürmer. Naturk. Verh. Holl. Maatsch. Wet. Harlem, 2. Verz. Deel 13, 112 pp. pl. 1–36A.

WARD, H. B.

1910. Internal Parasites of the Sebago Salmon. Bull. U. S. Bur. Fish., 28: 1153–94, 1 pl.

WEINLAND, D. F.

1858. Human cestoides, an essay on the tapeworms of man. 103 pp. Camb. (Mass.).

WILLEMOES-SUHM, R.

1869. Helminthologisches Notizen I. 1. Zur Entwickelung von *Schistocephalus dimorphus* Creplin. Zeit. wiss. Zool., 19:470–72.

1870. Helminthologisches Notizen II. Zeit. wiss. Zool., 20:94–98, Taf. X.

WOLF, E.

1906. Beiträge zur Entwickelungsgeshichte von *Cyathocephalus truncatus* Pallas. Zool. Anz., 30:37–45.

WOLFFHÜGEL, K.

1900. Beitrag zur Kenntnis der Vogelhelminthen. Diss. (Basel), 204 pp., 7 pl.

YOUNG, R. T.

1913. The Histogenesis of the Reproductive Organs of *Taenia pisiformis*. Zool. Jahrb., Anat., 35:355–418.

ZEDER, J. G. H.

1800. Erster Nachtrag zur Naturgeschichte der Eingeweidewürmer, mit Zufassen und Anmerkungen herausgegeben. 340 pp., 6 pl. Leipzig.

1803. Anleitung zur Naturgeschichte der Eingeweidewürmer. 448 pp., 4 pl. Bamberg.

ZENECKE, E.

1895. Untersuchungen über den feinern Bau der Cestoden. Zool. Jahrb., Anat., 25: 91-161, pl. 8-15.

ZSCHOKKE, F.

1884. Recherches sur l'organisation et la distribution zoologique des vers parasites des poissons d'eau douce. Arch. biol., 5:154–243.

1896. Zur Faunistik der parasitischen Würmer von Süsswasserfischen. Centrbl. Bakt. Parasit., 19:772–84, 915–25.

1903. Die arktischen Cestoden. Fauna Arct., 3; 31 pp., 2 pl.

1903a. Marine Schmarotzer in Süsswasserfischen. Verh. naturf. Ges. Basel. 16:118–57, 2 pl.

EXPLANATION OF PLATES

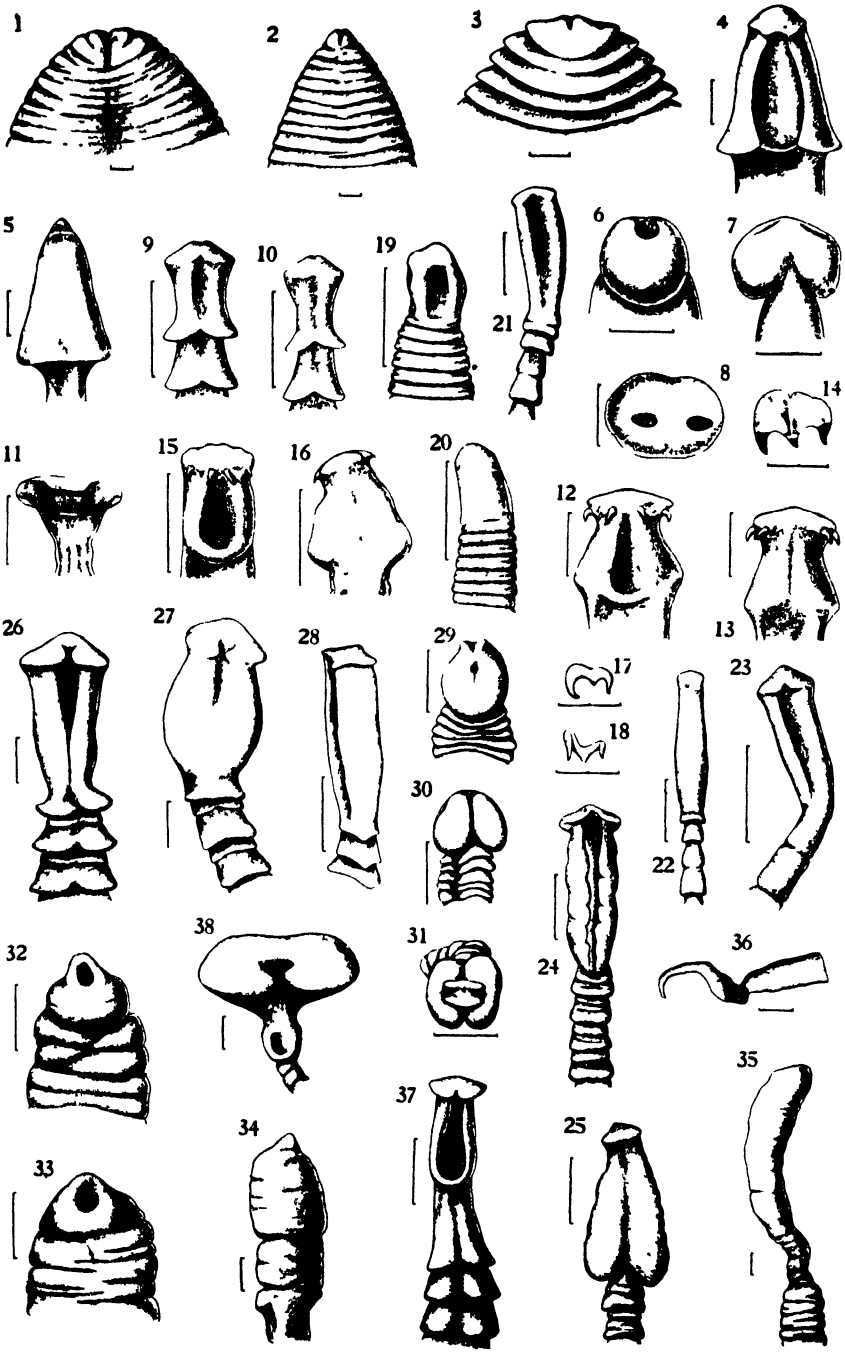
ABBREVIATIONS

bc	bothrial cavity	*ns*	nerve strand
bo	bothrial opening	*o*	ovary
bs	bothrial sphincter	*oc*	oocapt
c	cirrus	*od*	oviduct
cm	circular muscles	*ot*	ootype
cs	cirrus-sac	*p*	proboscis
cu	cuticula	*rs*	receptaculum seminis
cvd	common vitelline duct	*s*	subcuticula
dk	hermaphroditic duct	*t*	testis
dm	dorsoventral muscles	*td*	terminal disc
ec	excretory canal	*tm*	transverse muscles
ed	ejaculatory duct	*ud*	uterine duct
ev	excretory vesicle	*uo*	uterus opening
fa	female atrium	*us*	uterus sac
fd	fertilization duct	*ut*	uterus
g	genitalia	*v*	vagina
ga	genital atrium	*vb*	vestibule
gc	ganglionic cells	*vd*	vas deferens
io	isthmus of ovary	*vg*	vitelline glands
lm	longitudinal muscles	*vo*	vaginal opening
nc	nerve commissure	*vs*	vesicula seminalis

The lines in the figures have the following values: 0.05mm. in figures 63, 67, 105, 106, 107, 108; 0.2mm. in figures 14, 17, 18, 88, 94, 97, 99, 101; and 0.5mm. in all other figures, unless otherwise stated in the explanation of the figure

EXPLANATION OF PLATE

Fig. 1. *Ligula intestinalis*, anterior end of larva, showing scolex.
Fig. 2. *Ligula intestinalis*, anterior end of adult.
Fig. 3. *Schistocephalus solidus*, anterior end of larva.
Fig. 4. *Marsipometra hastata*, scolex, surficial view.
Fig. 5. *Marsipometra hastata*, same specimen, lateral view.
Fig. 6. *Bothrimonus intermedius*, scolex, surficial view.
Fig. 7. *Bothrimonus intermedius*, same specimen, lateral view.
Fig. 8. *Bothrimonus intermedius*, same specimen, terminal view.
Fig. 9. *Haplobothrium globuliforme*, secondary scolex, surficial view.
Fig. 10. *Haplobothrium globuliforme*, same specimen, lateral view.
Fig. 11. *Cyathocephalus americanus*, scolex, toto preparation.
Fig. 12. Triaenophorus, larva, *robustus* type, surficial view.
Fig. 13. Triaenophorus, same specimen, lateral view.
Fig. 14. Triaenophorus, same specimen, one of the tridents of hooks.
Fig. 15. Triaenophorus, larva, *nodulosus* type, surficial view.
Fig. 16. Triaenophorus, same specimen, lateral view.
Fig. 17. Triaenophorus, same specimen, a trident, terminal view.
Fig. 18. Triaenophorus, same specimen, surficial view.
Fig. 19. *Bothriocephalus claviceps* from *Eupomotis gibbosus*, scolex, surficial view.
Fig. 20. *Bothriocephalus claviceps*, same specimen, lateral view.
Fig. 21. *Bothriocephalus scorpii*, scolex, surficial view.
Fig. 22. *Bothriocephalus scorpii*, same specimen, lateral view.
Fig. 23. *Bothriocephalus claviceps* from *Anguilla rostrata*, scolex, surficial view.
Fig. 24. *Bothriocephalus cuspidatus*, scolex, surficial view.
Fig. 25. *Bothriocephalus cuspidatus*, same specimen, lateral view.
Fig. 26. *Bothriocephalus manubriformis*, scolex, surficial view.
Fig. 27. *Bothriocephalus manubriformis*, same specimen, lateral view.
Fig. 28. *Bothriocephalus occidentalis*, scolex. After Linton.
Fig. 29. *Clestobothrium crassiceps*, scolex, surficial view.
Fig. 30. *Clestobothrium crassiceps*, same specimen, lateral view.
Fig. 31. *Clestobothrium crassiceps*, same specimen, terminal view.
Fig. 32. *Abothrium rugosum*, scolex of young strobila.
Fig. 33. *Abothrium rugosum*, later stage in degeneration of same.
Fig. 34. *Abothrium rugosum*, still later stage.
Fig. 35. *Abothrium rugosum*, pseudoscolex from lumen of pyloric coecum of host.
Fig. 36. *Abothrium rugosum*, pseudoscolex from wall of coecum.
Fig. 37. *Abothrium crassum*, scolex from *Cristivomer namaycush*.
Fig. 38. *Abothrium crassum*, enlarged scolex from *Lota maculosa*.

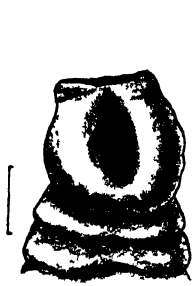


COOPER PSEUDOPHYLLIDEAN CESTODES PLATE I

PLATE II

EXPLANATION OF PLATE

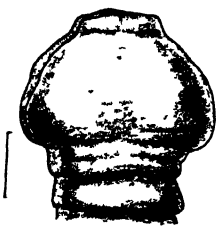
Fig. 39. *Abothrium crassum*, scolex of specimen from *Salmo salar*, surficial view.
Fig. 40. *Abothrium crassum*, same specimen, lateral view.
Fig. 41. *Abothrium crassum*, young scolex from *Lota maculosa*.
Fig. 42. *Abothrium crassum*, same specimen, lateral view.
Fig. 43. *Haplobothrium globuliforme*, primary scolex, toto preparation.
Fig. 44. *Haplobothrium globuliforme*, primary strobila, toto preparation.



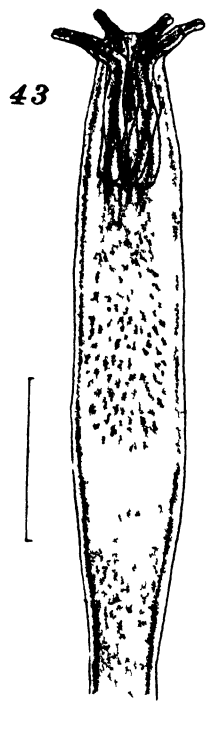
39

41

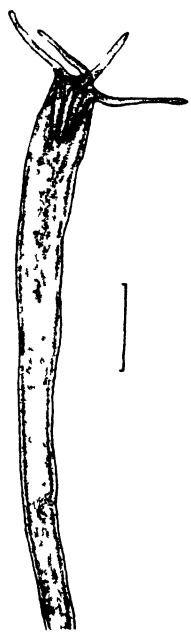
42

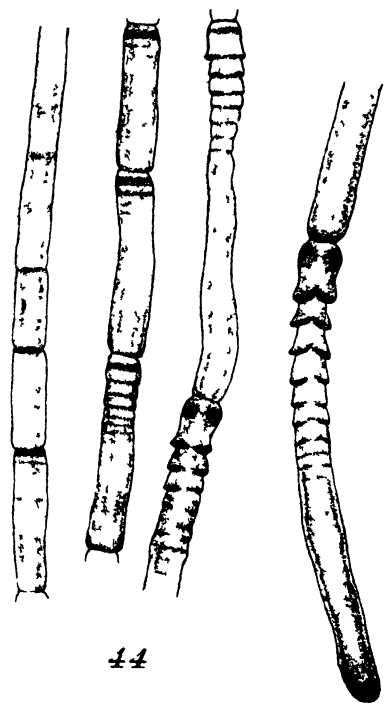


40



43



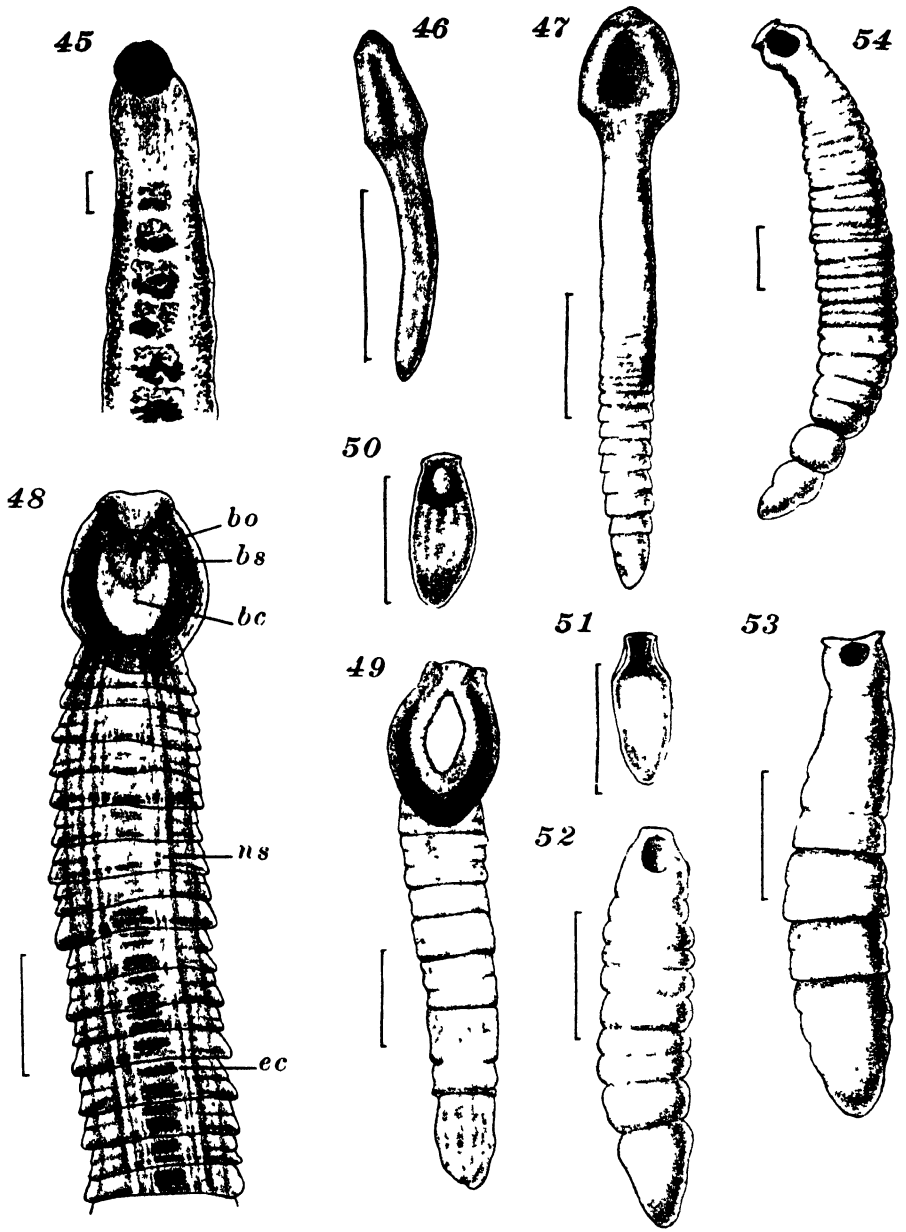


44

PLATE III

EXPLANATION OF PLATE

Fig. 45. *Bothrimonus intermedius*, scolex and anterior end, toto preparation, showing foremost sets of genitalia.
Fig. 46. *Marsipometra hastata*, plerocercoid, surficial view.
Fig. 47. *Marsipometra hastata*, older plerocercoid, surficial view.
Fig. 48. *Clestobothrium crassiceps*, toto of scolex and anterior end.
Fig. 49. *Clestobothrium crassiceps*, toto of young strobila, surficial view.
Fig. 50. *Abothrium crassum*, plerocercoid from *Cristivomer namaycush*, surficial view.
Fig. 51. *Abothrium crassum*, same specimen, lateral view.
Fig. 52. *Abothrium crassum*, young strobila from same host.
Fig. 53. *Abothrium crassum*, older strobila from same host.
Fig. 54. *Abothrium crassum*, still older strobila, showing dropping off of segments posteriorly.



COOPER PSEUDOPHYLLIDEAN CESTODES PLATE III

PLATE IV

EXPLANATION OF PLATE

Fig. 55. *Bothriocephalus scorpii*, three anterior primary segments, toto preparation. The stars at the side indicate the extent of the segments.

Fig. 56. *Bothriocephalus scorpii*, one farther back, also toto.

Fig. 57. *Bothriocephalus scorpii*, another, showing reproductive rudiments.

Fig. 58. *Clestobothrium crassiceps*, primary segment with reproductive rudiments, toto preparation.

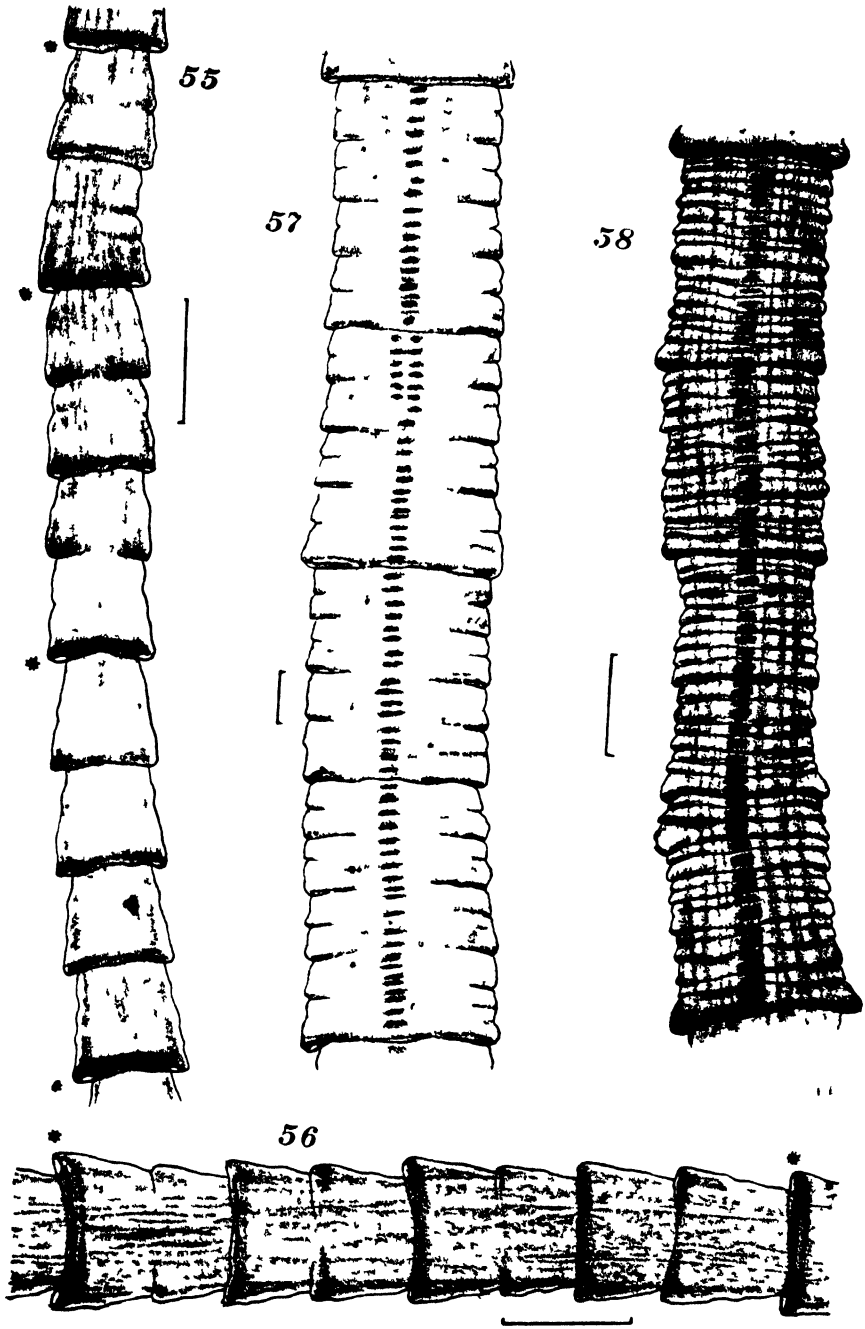
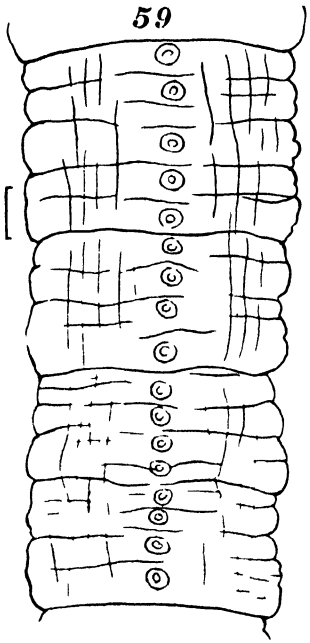
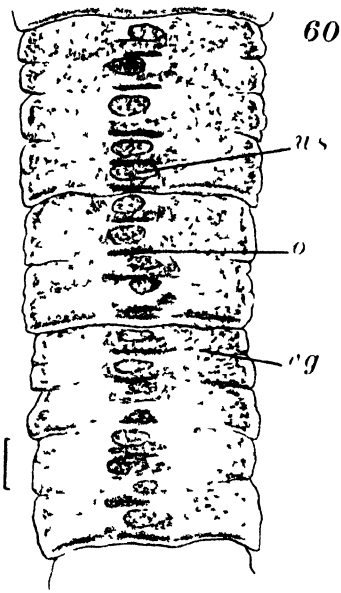

55
57
58
56

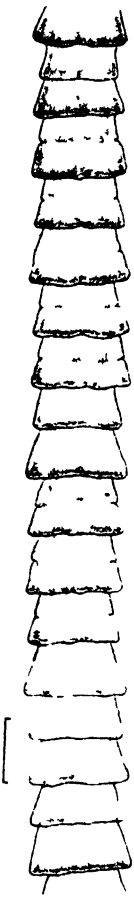
PLATE V

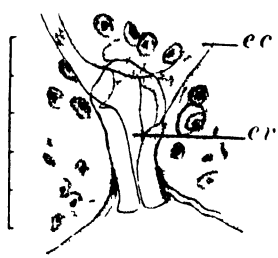
EXPLANATION OF PLATE

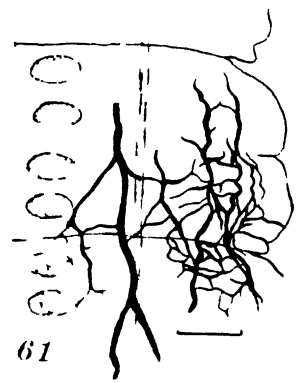
Fig. 59. *Bothriocephalus scorpii*, outline of mature segments.
Fig. 60. *Bothriocephalus scorpii*, toto of same specimen.
Fig. 61. *Bothriocephalus scorpii*, portion of strobila showing excretory vessels.
Fig. 62. *Bothriocephalus manubriformis*, anterior primary segment.
Fig. 63. *Abothrium rugosum*, terminal excretory vesicle.
Fig. 64. *Abothrium crassum*, anterior segments of strobila from *Coregonus clupeiformis*, toto.


59


60
us
o
cg


64


63
ec
cr


61

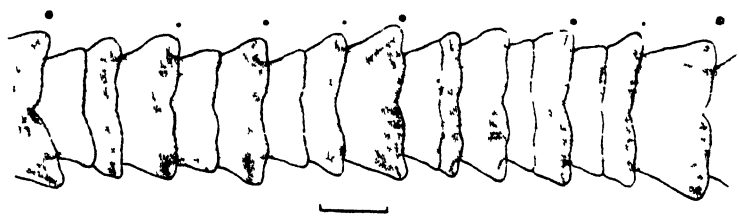

62

PLATE VI

EXPLANATION OF PLATE

Fig. 65. *Haplobothrium globuliforme*, transection thru primary scolex.

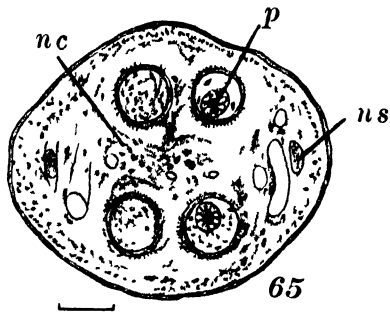
Fig. 66. *Haplobothrium globuliforme*, transection thru the ganglionic mass behind the proboscides. The reference line is 0.1mm. long.

Fig. 67. *Haplobothrium globuliforme*, transection thru a single proboscis bulb.

Fig. 68. *Marsipometra hastata*, toto of ripe proglottis.

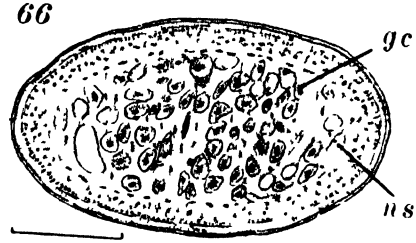
Fig. 69. *Bothriocephalus cuspidatus*, transection thru an anterior segment.

Fig. 70. *Bothriocephalus cuspidatus*, toto of ripe proglottides, posterior in deeper optical section.

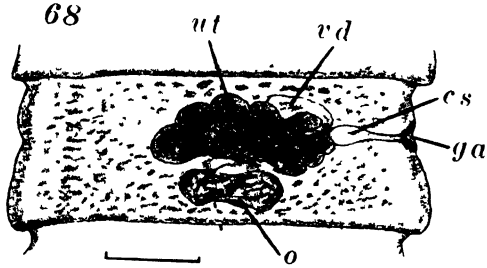


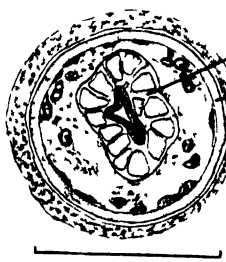
65

66



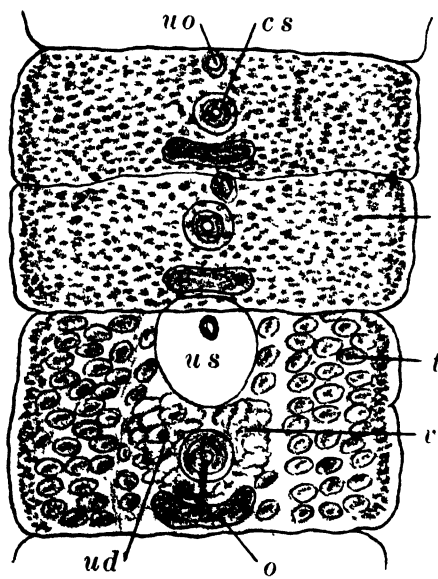
68

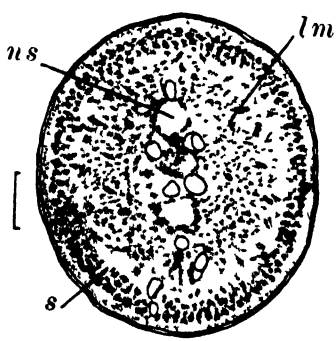




67

70



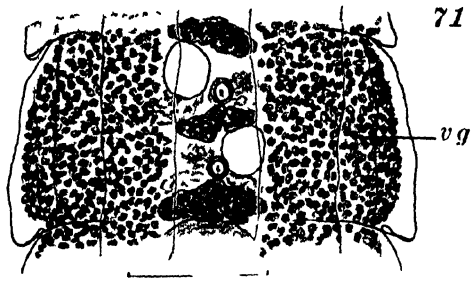


69

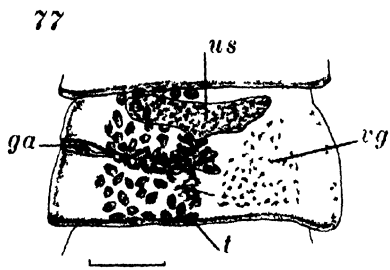
PLATE VII

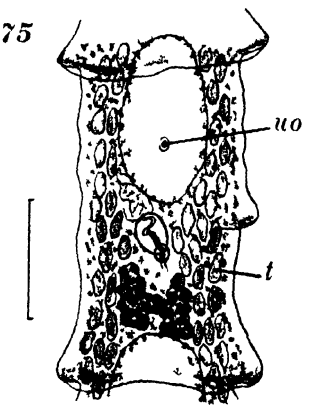
EXPLANATION OF PLATE

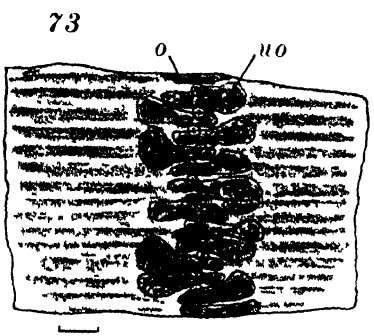
Fig. 71. *Bothriocephalus scorpii*, toto of two segments.
Fig. 72. *Bothriocephalus claviceps* from *Eupomotis gibbosus*, toto of mature proglottides.
Fig. 73. *Bothriocephalus manubriformis*, toto of mature proglottides.
Fig. 74. *Clestobothrium crassiceps*, segments showing spurious articulations.
Fig. 75. *Clestobothrium crassiceps*, toto of mature proglottis.
Fig. 76. *Abothrium rugosum*, frontal section of mature proglottis.
Fig. 77. *Abothrium crassum*, toto of ripe proglottis of strobila from *Coregonus clupeiformis*.

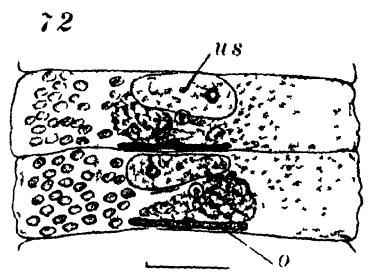

71
vg

74


77
us
ga
vg
t


75
uo
t


73
o
uo


72
us
o

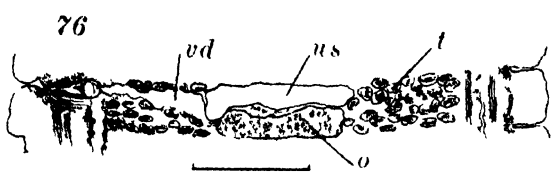
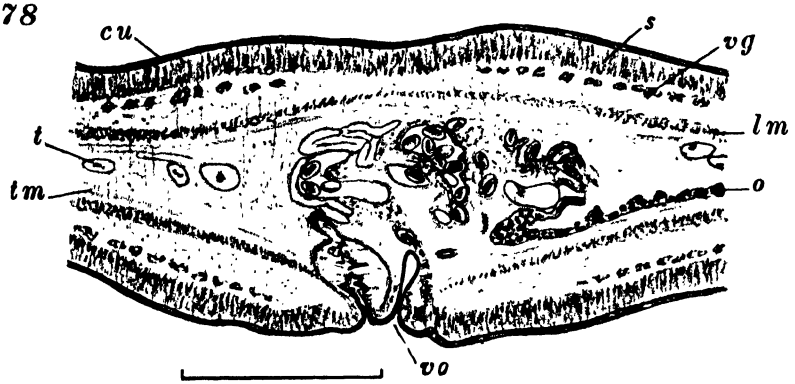

76
vd
us
t
o

PLATE VIII

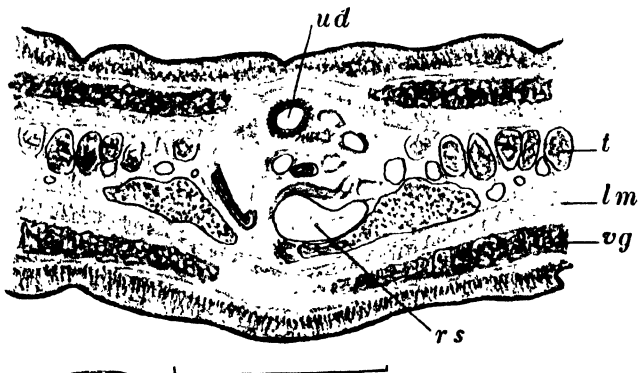
EXPLANATION OF PLATE

Fig. 78. *Ligula intestinalis*, median portion of a transection thru the genital cloaca.
Fig. 79. *Schistocephalus solidus*, median portion of transection thru ovary.
Fig. 80. *Schistocephalus solidus*, median portion of transection thru the seminal vesicle and cirrus-sac. The reference line is 0.3mm. long.
Fig. 81. *Bothrimonus intermedius*, transection thru the ovarian isthmus.

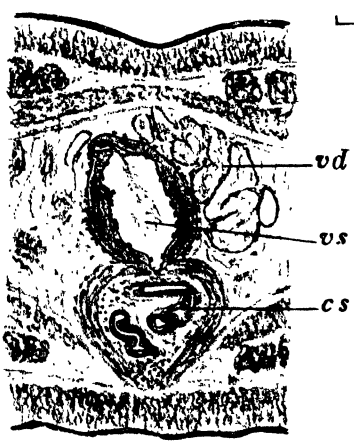
78



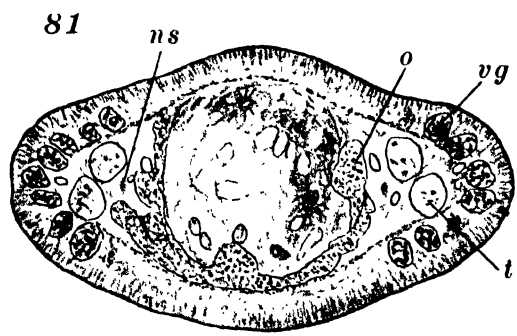
79



80



81



EXPLANATION OF PLATE

Fig. 82. *Cyathocephalus americanus*, transection thru ovarian isthmus.
Fig. 83. *Marsipometra hastata*, transection thru ovarian isthmus.
Fig. 84. *Bothriocephalus scorpii*, transection thru ovary.
Fig. 85. *Bothriocephalus claviceps* from *Eupomotis gibbosus*, transection thru ovary.
Fig. 86. *Bothriocephalus cuspidatus*, transection thru ovary of mature proglottis.

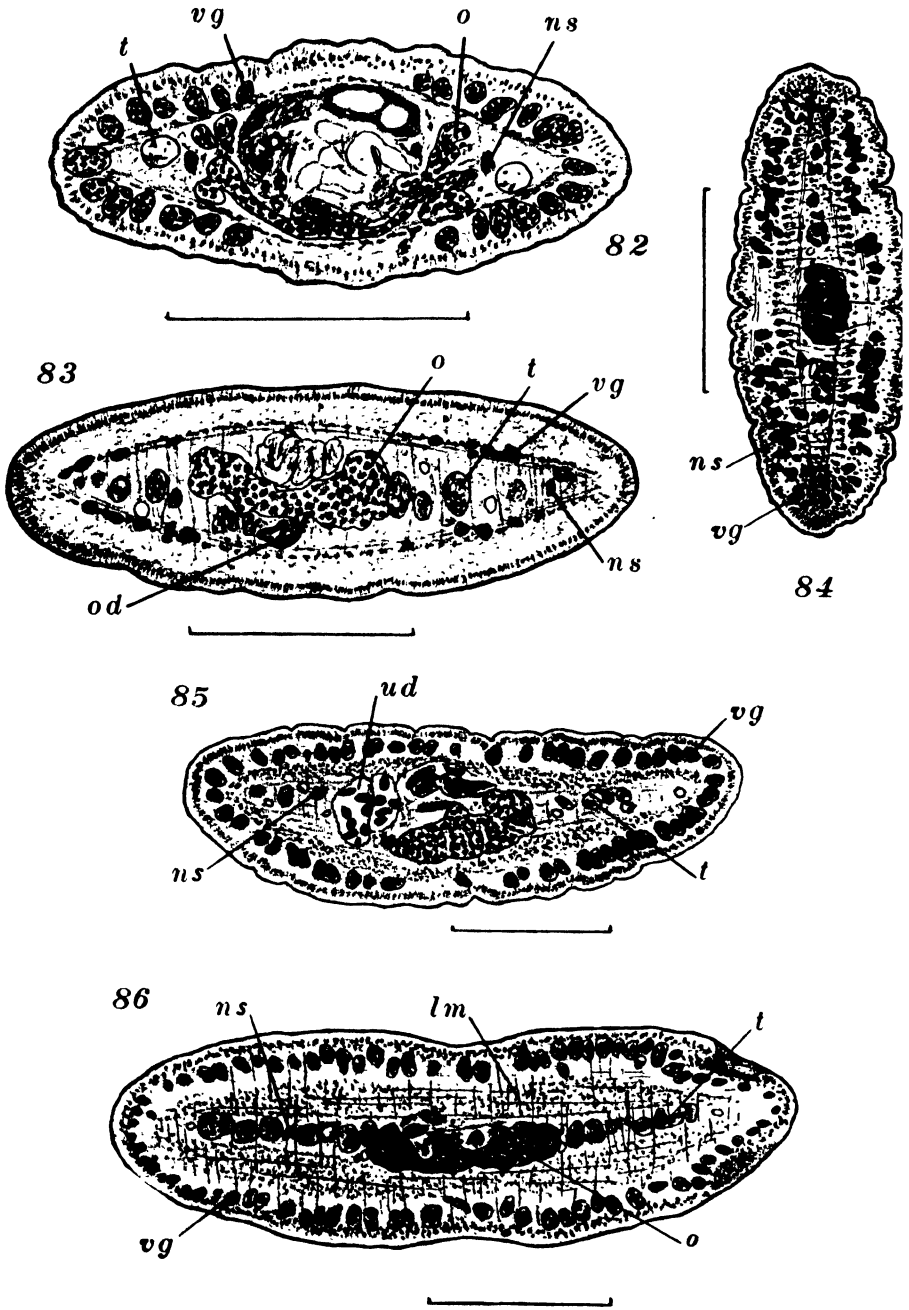
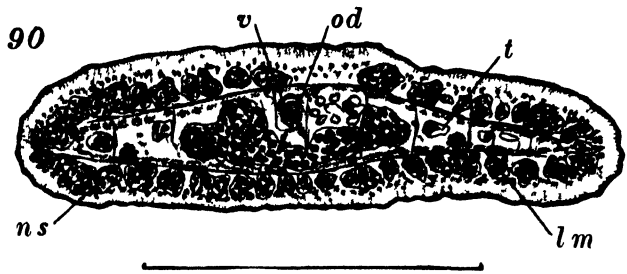
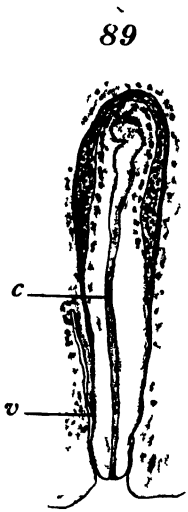

vg
o
ns
t
82
83
o
t
vg
ns
od
84
ns
vg
85
ud
vg
ns
t
86
ns
lm
t
vg
o

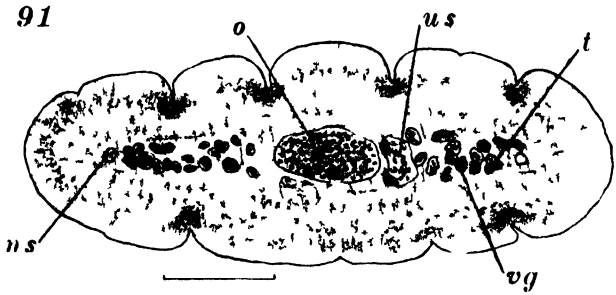
PLATE X

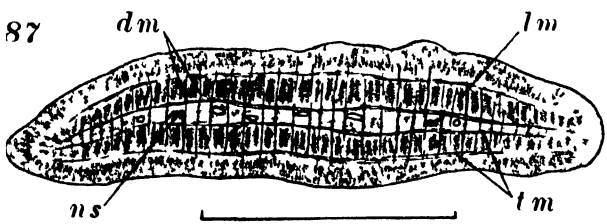
EXPLANATION OF PLATE

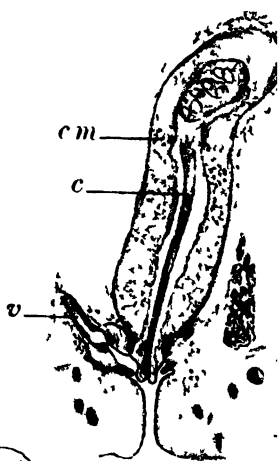
Fig. 87. *Bothriocephalus manubriformis*, transection thru anterior region.
Fig. 88. *Bothriocephalus manubriformis*, cirrus-sac and vaginal bulb from a transection.
Fig. 89. *Bothriocephalus occidentalis*, cirrus-sac from a transection. The reference line is 0.1mm long.
Fig. 90. *Clestobothrium crassiceps*, transection thru the ovary.
Fig. 91. *Abothrium rugosum*, transection thru the ovary.
Fig. 92. *Abothrium crassum*, transection thru the ovary of a specimen from *Salmo salar*.


90
v
od
t
ns
lm


89
c
v


91
o
us
t
ns
vg


87
dm
lm
ns
tm


cm
c
v
88

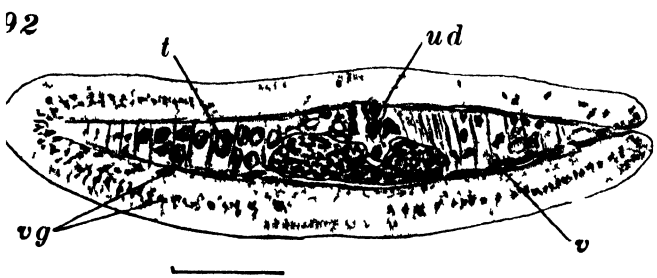
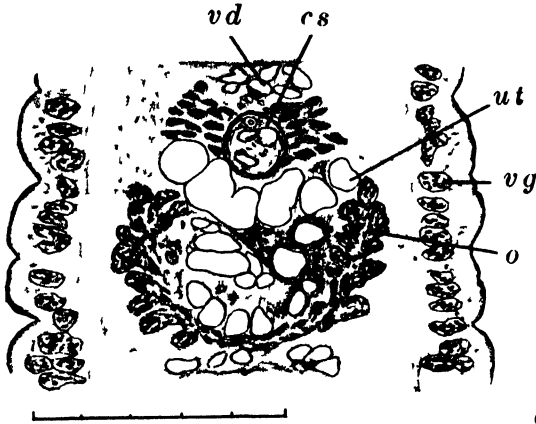

92
t
ud
vg
v

PLATE XI

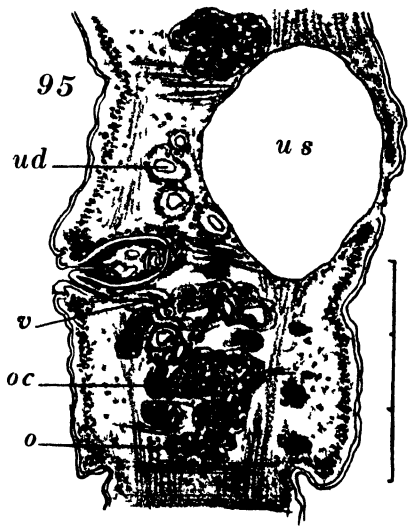
EXPLANATION OF PLATE

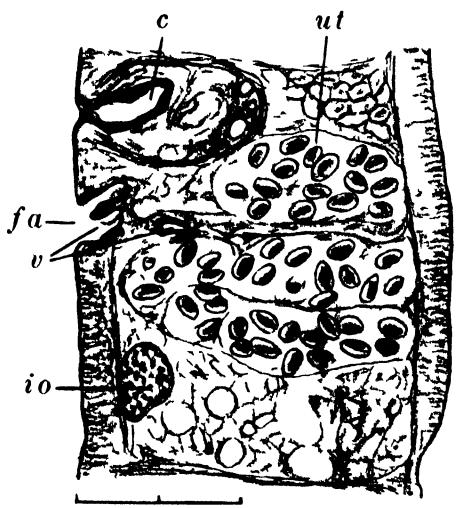
Fig. 93. *Cyathocephalus americanus*, frontal section of ripe proglottis.
Fig. 94. *Bothrimonus intermedius*, median sagittal section.
Fig. 95. *Bothriocephalus scorpii*, median sagittal section, composite. The reference line is 0.3mm. long.
Fig. 96. *Bothriocephalus claviceps* from *Eupomotis gibbosus*, median sagittal section.
Fig. 97. *Bothriocephalus manubriformis*, transection thru uterus opening.



93

97





94

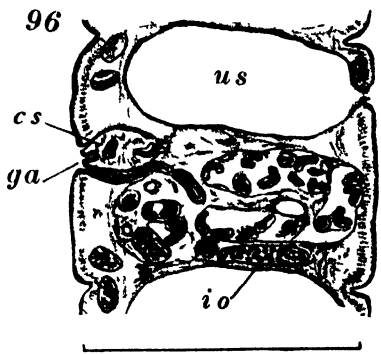


PLATE XII

EXPLANATION OF PLATE

Fig. 98. *Ligula intestinalis*, union of vagina and vitelline duct with oviduct. The reference line is 0.1mm. long.

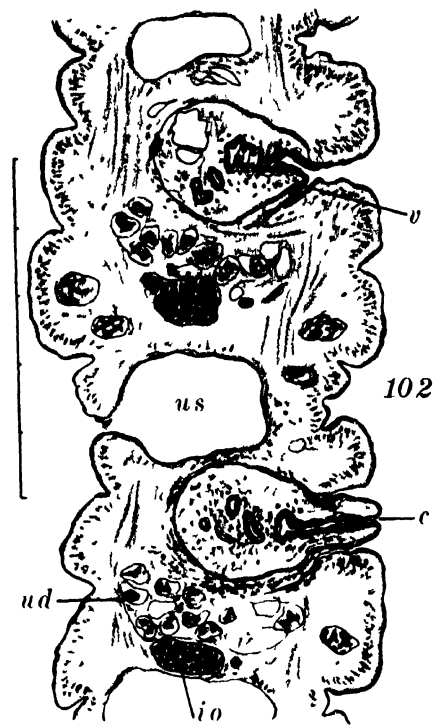
Fig. 99. *Cyathocephalus americanus*, oocapt containing an ovum.

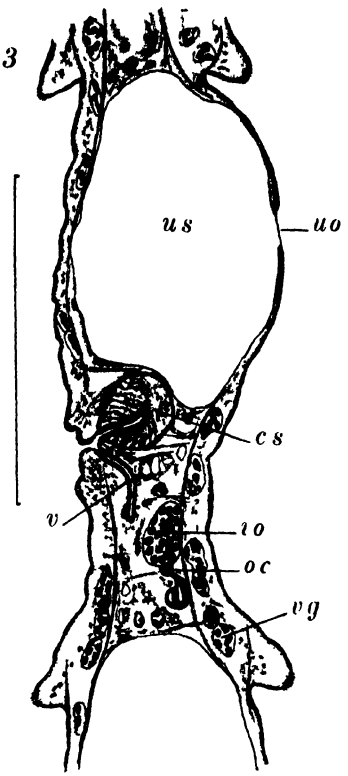
Fig. 100. *Marsipometra hastata*, genital cloaca from frontal section.

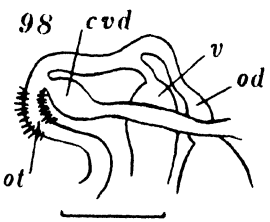
Fig. 101. *Marsipometra hastata*, cirrus sac from a transection.

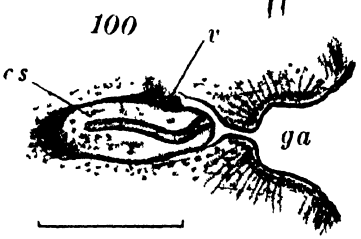
Fig. 102. *Bothriocephalus cuspidatus*, median sagittal section, composite.

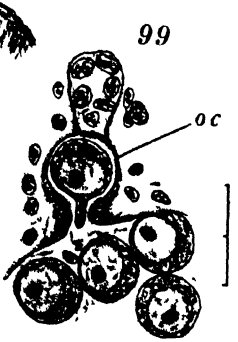
Fig. 103. *Clestobothrium crassiceps*, median sagittal section, composite.


v
us
102
c
ud
io


103
us
uo
cs
v
io
oc
vg


98
cvd
v
od
ot


100
v
cs
ga


99
oc

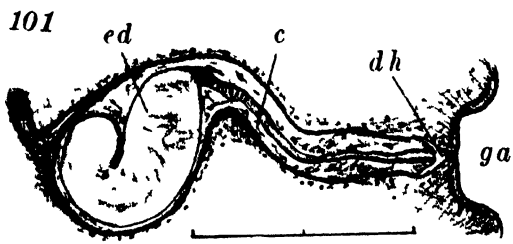

101
ed
c
dh
ga

PLATE XIII

EXPLANATION OF PLATE

Fig. 104. *Cyathocephalus americanus*, diagram of median sagittal section.

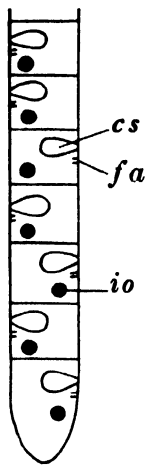
Fig. 105. *Bothriocephalus scorpii*, portion of section, showing union of vagina with oviduct.

Fig. 106. *Bothriocephalus cuspidatus*, young egg, showing an early stage in development, drawn from life.

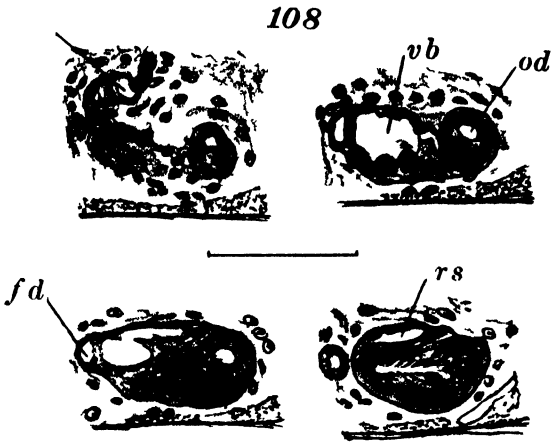
Fig. 107. *Bothriocephalus cuspidatus*, older egg, many-celled stage.

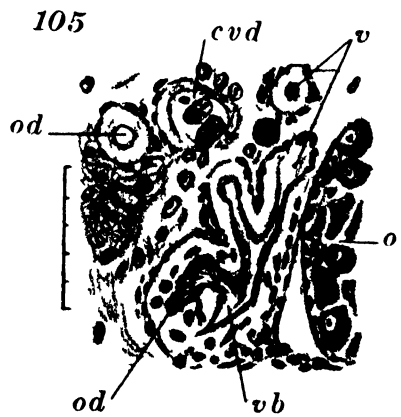
Fig. 108. *Clestobothrium crassiceps*, four consecutive sections thru union of vagina and oviduct, showing the receptaculum seminis.

Fig. 109. *Abothrium rugosum*, union of vagina and common vitelline duct with oviduct. The reference line is 0.02mm. long.

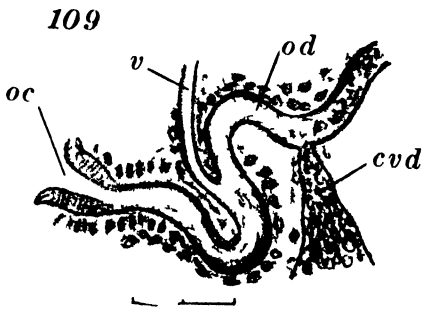


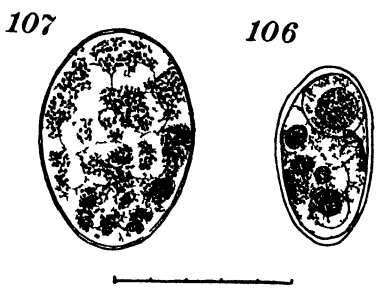
104

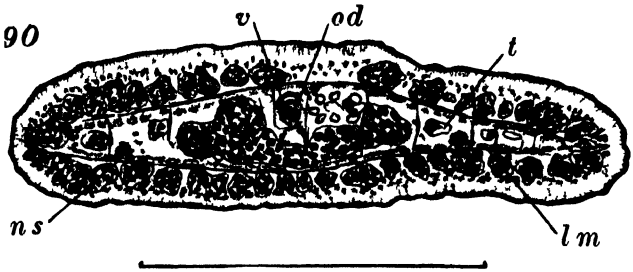


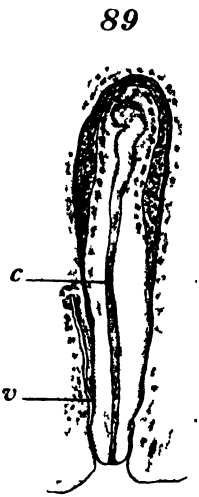


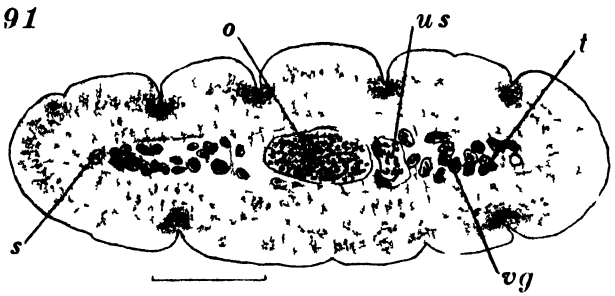
105

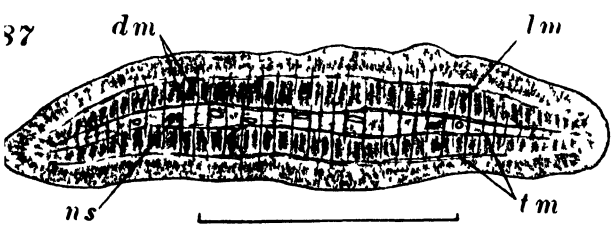


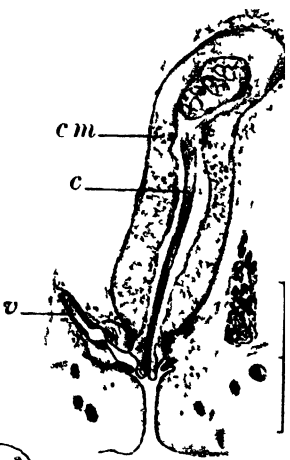



90
v
od
t
ns
lm


89
c
v


91
o
us
t
s
vg


37
dm
lm
ns
tm


cm
c
v
88

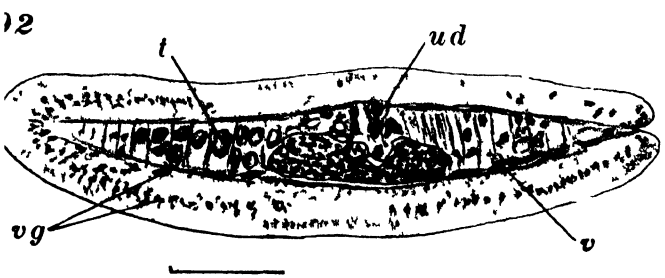
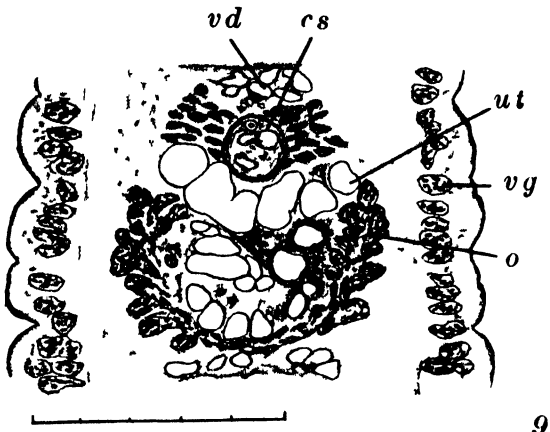

92
t
ud
vg
v

PLATE XI

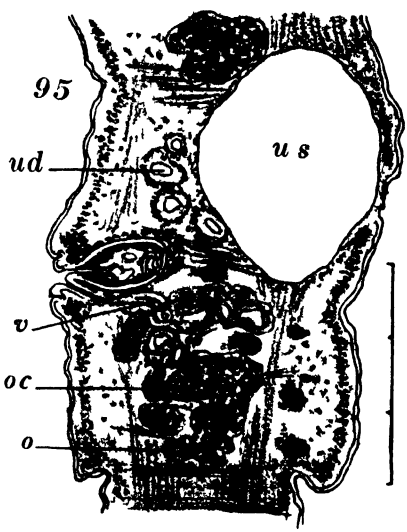
EXPLANATION OF PLATE

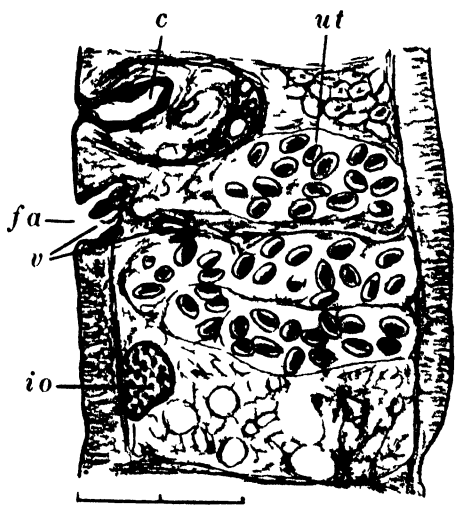
Fig. 93. *Cyathocephalus americanus*, frontal section of ripe proglottis.
Fig. 94. *Bothrimonus intermedius*, median sagittal section.
Fig. 95. *Bothriocephalus scorpii*, median sagittal section, composite. The reference line is 0.3mm. long.
Fig. 96. *Bothriocephalus claviceps* from *Eupomotis gibbosus*, median sagittal section.
Fig. 97. *Bothriocephalus manubriformis*, transection thru uterus opening.



93

97





94

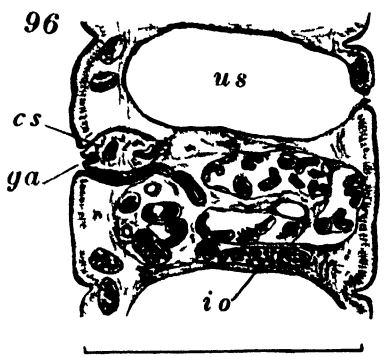


PLATE XII

EXPLANATION OF PLATE

Fig. 98. *Ligula intestinalis*, union of vagina and vitelline duct with oviduct. The reference line is 0.1mm. long.

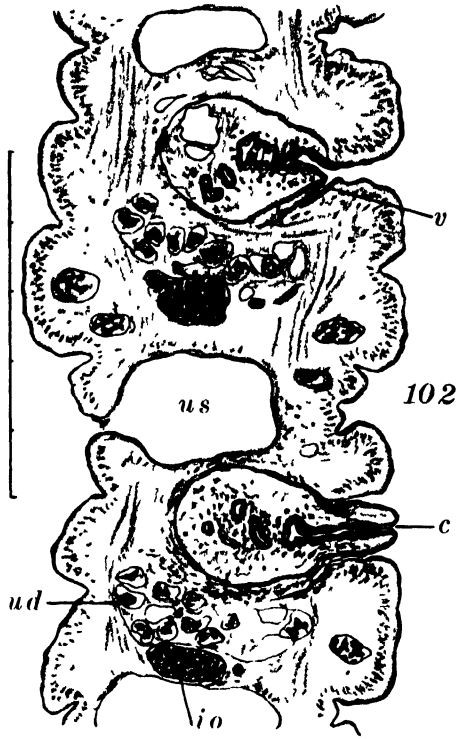
Fig. 99. *Cyathocephalus americanus*, oocapt containing an ovum.

Fig. 100. *Marsipometra hastata*, genital cloaca from frontal section.

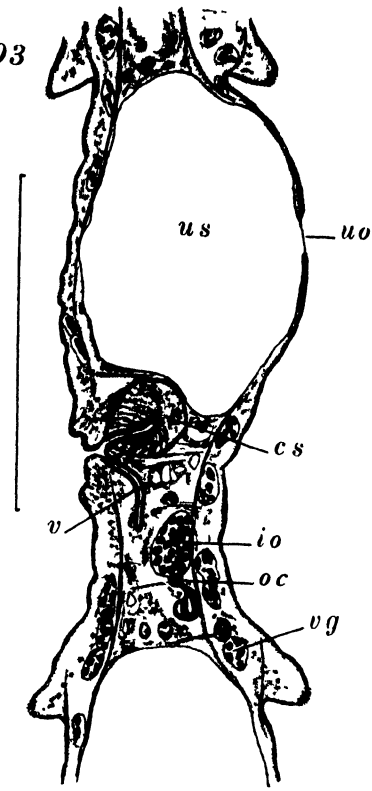
Fig. 101. *Marsipometra hastata*, cirrus sac from a transection.

Fig. 102. *Bothriocephalus cuspidatus*, median sagittal section, composite.

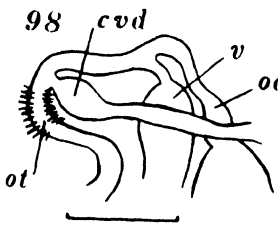
Fig. 103. *Clestobothrium crassiceps*, median sagittal section, composite.

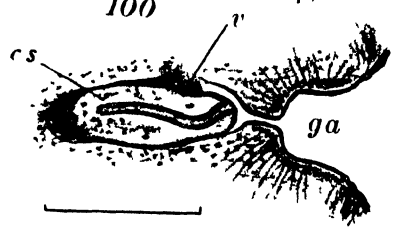

v
us
c
ud
io

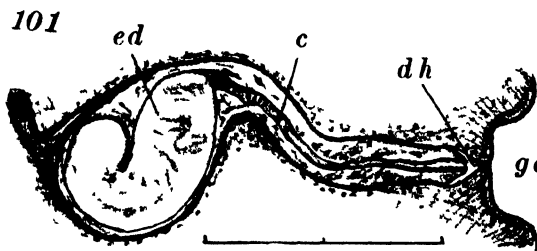
102


us
uo
cs
v
io
oc
vg

103


98
cvd
v
od
ot


100
v
cs
ga


101
ed
c
dh
ga

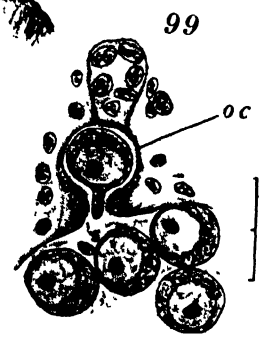

99
oc

PLATE XIII

EXPLANATION OF PLATE

Fig. 104. *Cyathocephalus americanus*, diagram of median sagittal section.

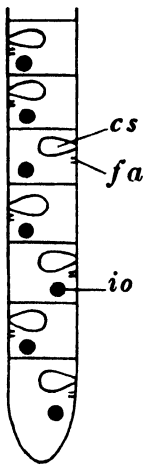
Fig. 105. *Bothriocephalus scorpii*, portion of section, showing union of vagina with oviduct.

Fig. 106. *Bothriocephalus cuspidatus*, young egg, showing an early stage in development, drawn from life.

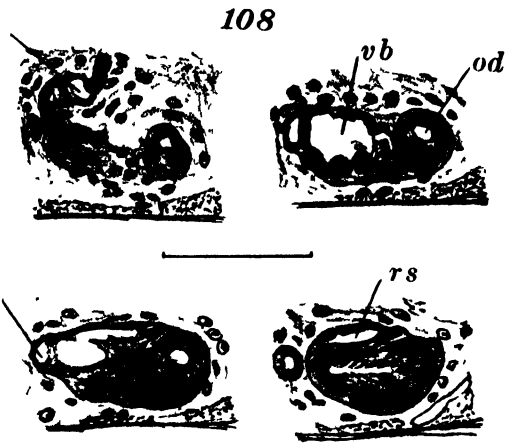
Fig. 107. *Bothriocephalus cuspidatus*, older egg, many-celled stage.

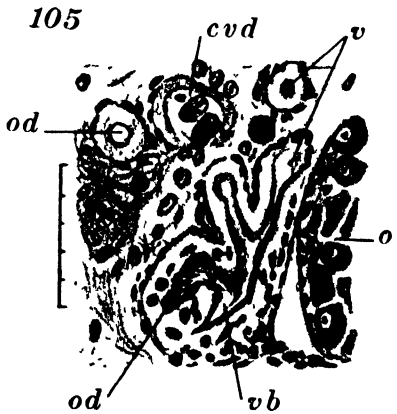
Fig. 108. *Clestobothrium crassiceps*, four consecutive sections thru union of vagina and oviduct, showing the receptaculum seminis.

Fig. 109. *Abothrium rugosum*, union of vagina and common vitelline duct with oviduct. The reference line is 0.02mm. long.

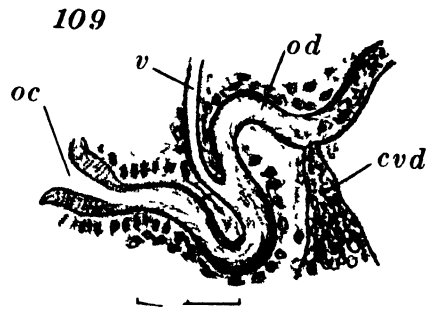


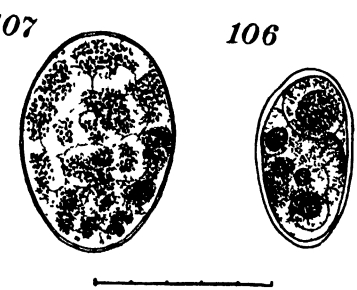
104





105





INDEX OF HOSTS

A

Abramis bjorkna, 23
  blicca, 23
  brama, 21
  vimba, 23
Acipenser oxyrhynchus, 64
  ruthenus, 99
  sturio, 64
Alburnus alburnus, 23
  lucidus, 21
Alca pica, 34
  torda, 33
Alosa ohiensis, 21
Ambloplites rupestris, 22
Ambystoma sp., 22
  tigrinum, 22
Ameiurus, 21
Amia, 71
Amia calva, 45
Amoetes branchialis, 23
Anas boschas fera, 22
  glacialis, 33
Anguilla acutirostris, 116
  anguilla, 116
  migratoria, 116
  rostrata, 116
  vulgaris, 99, 116
Aquila chrysaetus, 22
Ardea alba, 23
  ciconia, 23
  cinerea, 34
  egretta, 23
  nycticorax, 22
stellaris, 33
Arnoglossus boscii, 98
  pegosa, 98
  solea, 98
Aspius alburnus, 23
  rapax, 21
Atherina mocho, 21

B

Bass, white, 87
Blicca bjorkna, 21
Bothus maculatus, 99
Brochet, 83

C

Carassius carassius, 23
  gibelio, 21
  vulgaris, 23
Catostomus ardens, 21
  commersonii, 25, 85, 87
commersonii commersonii, 22
  latipinnis, 21
Chondrostoma nasus, 21
Ciconia alba, 22, 33
  ciconia, 23, 34
  nigra, 34
Clupea harengus, 189
  harengus membras, 199
Cobitis aculeata, 23
  taenia, 21
Colymbus arcticus, 22, 34
  auritus, 23
  cristatus, 23, 34
  glacialis, 34
  griseigena, 23, 34
  hoelbeelli, 23
  immer, 34
  rubricollis, 23
  septentrionalis, 33
  subcristatus, 23
  troile, 34
Coregenus albula, 83
  clupeiformis, 54, 189
  fera, 188
  lavaretus, 83, 188
  oxyrhynchus maraena, 189
  wartmanni, 21
Corvus corax, 34
  cornix, 22, 33
Cottus bairdii, 33
  bubalis, 98
  poecilopus, 33
  quadricornis, 98
  scorpio, 33
  scorpius, 97, 98
Cristivomer namaycush, 189
Cyprinus alburnus, 21
  blicca, 23
  brama, 23
  carassius, 23
  gobelio, 23
  lacustris, 23
  leuciscus, 23
  tinca, 23

D
Decapterus punctatus, 99
E
Esox lucius, 21, 83, 84, 86, 189
masquinongy, 85, 87
Eupomotis gibbosus, 116
F
Falco albicilla, 22
chrysaetos, 23
fulvus, 23
Fulica atra, 33
Fuligula clangula, 22
marila, 33
G
Gadidae, 178
Gadus aeglifinus, 98, 173
callarias, 173, 174
euxinus, 155
lota, 173
merluccius, 155, 173
minutus, 98
morrhua, 173, 174
morrua, 183
mustela, 173
pollachius, 174
Gammarus pulex, 61
Gasterosteus aculeatus, 33
bispinosus, 116
bispinosus atkinsii, 22, 33
cataphractus, 33
pungitius, 33
Gobio fluviatilis, 23
gobio, 21
vulgaris, 21
Graculus carbo, 22
H
Haematopus ostrealegus, 33
Hake, small, 155
Haliaetus albicilla, 22
Harelda glacialis, 33
Hemitripterus americana, 99, 100
Herodias alba, 22
Herring, lake, 86
Hiodon alosoides, 124
tergisus, 124
Hippoglossus hippoglossus, 99
Histiophorus gladius, 134, 146
sp., 134
Hybognathus nuchalis, 21
Hydrochelidon nigra, 22
I
Istiophorus nigricans, 134
L
Labrus maculatus, 99
Larus argentatus, 22, 34
canus, 23
capistranus, 34
marinus, 34
melanocephalus, 23
parasiticus, 23
pelecanus carbonis, 23
pygmaei, 23
ridibundus, 33
tridactylus, 23
Leucichthys artedi, 83, 84, 86
Leuciscus erythrophthalmus, 23
leuciscus, 23
phoxinus, 23
pulchellus, 23
rutilis, 21
vulgaris, 23
Limanda ferruginea, 99
Lophodytes cucullatus, 33
Lophopsetta maculata, 99
Lota, 178
Lota lota, 189
maculosa, 41, 86, 189, 194
molva, 183
vulgaris, 99, 174, 189
Lucioperca lucioperca, 23
sandra, 21
M
Melanogrammus aeglifinus, 174
Merganser, 22
Merganser merganser, 23, 34
sp., 23
Mergus albellus, 23, 34
merganser, 22
minutus, 23
serrator, 22, 33
Merlangus carbonarius, 155, 174
pollachius, 183
sp., 155
Merluccius bilinearis, 112, 155, 170
esculentus, 155
merluccius, 155
vulgaris, 155, 174
Microgadus tomcod, 63, 174
Micropterus dolomieu, 22, 85, 87
Mola, 91
Mola mola, 92
Morrhua aeglifinus, 174
americana, 21
vulgaris, 174
Motella mustela, 99, 183
Mullus barbatus, 99
Muraena anguilla, 116
cassini, 116

Myoxocephalus aeneus, 99, 100
groenlandicus, 100
octodecimspinosus, 99

N

Nemachilus strauchi, 21
Notropis cayuga, 22
cornutus, 21, 22
delicatus, 87
hudsonius, 22
Nycticorax nycticorax, 22
Nyroca marila, 33

O

Osmerus mordax, 21
operlanus, 189

P

Paralichthys dentatus, 99
oblongus, 99
Palinurichthys perciformis, 99
Perca flavescens, 22, 87, 124
fluviatilis, 21, 189
Percina caprodes, 124
Petromyzon branchialis, 21
Phoca vitulina, 21, 33
Pickerel, 124
Platessa flesus, 98
passer, 98
plana, 98
Pleuronectes boscius, 98
flesus, 98
maximus, 98
rhombus, 98
solea, 98
Podiceps auritus, 22
cristatus, 24, 34
minor, 23
nigricollis, 33
rubricollis, 23, 34
Podilymbus podiceps, 23
Polyodon, 71
Polyodon spathula, 72
Pomatomus saltatrix, 155
Pomolobus aestivalis, 170
Pontoporeia hoyi, 61
Poronotus triacanthus, 112
Psetta maxima, 98
Pseudopleuronectes americanus, 64, 99
Puffinus kuhli, 33

R

Raja clavata, 99
Rana esculenta, 33
Recurvirostra avocetta, 33
Rhombus barbue, 99
laevis, 99
maximus, 98, 99
moeoticus, 99
Rhynchichthys gronovii, 33
Rissa tridactyla, 22
Rock cod, 149

S

Salmo alipinus, 188
carpio, 188
caspius, 188
fario, 188
hucho, 188
lacustris, 188
namaycush, 188
salar, 33, 113, 183, 187, 188, 189, 194
salaris, 190
salar nobilis, 188
salar sebago, 188
salvelinus, 21, 188
siscowet, 188
thymallus, 188
thymallus vexillifer, 188
trutta, 188
umbla, 188
Salvelinus fontinalis, 189
Scardinius erythrophthalmus, 21
Schizopygopsis kozlovi, 21
Scomber scomber, 100
Scorpaena porcus, 99, 113
scrofa, 112
Scyllium canicula, 163
Sebastodes sp., 149
Siluris glanis, 21
Solea monochii, 99
Squalius cephalus, 21
turcicus, 23
Stercorarius parasitica, 22, 33
Sterna arctica, 34
hirundo, 22, 33
macroura, 34
minuta, 34
nigra, 23, 34
Stizostedion canadense, 85, 87, 124
vitreum, 86, 87, 124
Sunfish, 91

T

Tarpon atlanticus, 134, 145
Tetrapterus albidus, 134
belone, 134
imperator, 134
sp., 145
Thymallus vulgaris, 189
Tinca vulgaris, 21
Torpedo ocellata, 98

Totanus calidrus, 33
chloropus, 23
Trachurops crumenophthalmus, 100
Trigla adriatica, 98
lineata, 98
Trout, 189
Trutta fario, 189
lacustris, 189
salar, 189
trutta, 189
variabilis, 189
vulgaris, 198

U

Uria grylle, 34
troile, 33
Uranidea formosa, 33
Urinator arcticus, 22, 33
stellatus, 23
Urophycis chuss, 100
tenuis, 174

X

Xema minutum, 22
ridibundum, 23
Xiphias gladius, 91

INDEX

A

Abothrium, 171, 176
Abothrium crassum, 12, 78, 176 186
gadi, 172
rugosum, 12, 74, 172, 193
Acanthocephala, 51
Acanthophallidae, 15
Acrobothrium, 53
Alyselminthus, 95
Alyselminthus bipunctatus, 96
Amphicotyle, 171
Amphicotyle heteropleura, 159, 193
Amphicotylinae, 12 171
Amphitretidae, 15
Anchistrocephalus, 70
Anonchocephalus, 70
Aprocta, 9

B

Bothriudium, 16, 70
Bothridium pithonis, 16
Bothrimonus, 11, 62
Bothrimonus cohaerens, 64
fallax, 64, 66
intermedius, 11, 63
nylandicus, 60, 63, 64
pachycephalus, 60, 64
sturionis, 62, 64
Bothriocephalidae, 9
Bothriocephalidea, 9
Bothriocephalus, 95
Bothriocephalus affinis, 113
angustatus, 114
bipunctatus, 96
claviceps, 12, 101, 198, 114
crassiceps, 154
cuspidatus, 12, 94, 123, 135, 195
dubius, 101
du Saumon, 186
fasciatus, 101
gadi merluccii, 163
histiophorus, 133, 147
imbricatus, 197
infundibuliformis, 185, 186
laciniatus, 133, 145, 150
manubriformis, 12, 133, 145, 147, 149
neglectus, 158
nodosus, 31
occidentalis, 12, 145, 149
pilula, 154
plicatus, 89
proboscideus, 176, 186
punctatus, 96, 112, 118, 195
punctatus forma bubalidis, 96
forma cottiquadricornis, 96
forma motellae, 96
forma punctatus vel typica, 96
forma rhombi, 96
rugosus, 172
sagittatus, 184
salmonis umblae, 186
scorpii, 12, 43, 49, 93, 96, 112, 119, 125, 135, 152, 159, 193
scorpii forma bubalidis, 112
forma motellae, 112
semiligula, 19
solidus, 30
spiraliceps, 164
suecicus, 186
truncatus, 89
variabilis, 101
zschokkei, 31
Bothriotaenia, 70, 88, 184
Bothriotaenia gadi, 184
hastata, 71
infundibuliformis, 186
plicata, 89
proboscidea, 183, 186
rugosa, 172

C

Caryophyllaeidae, 7, 13
Cephalocotylea, 9, 62
Cephalocotyleum, 53
Ceatoda, 10
Cestodaria, 10
Cestodes, 9
Clestobothrium, 12, 153
Clestobothrium crassiceps, 12, 65, 94, 103, 140, 154
Cyathocephalinae, 11, 53, 88
Cyathocephalus, 11, 53, 70
Cyathocephalus americanus, 11, 53, 66
catenatus, 56
truncatus, 42, 53
Cysticercus, 81
Cysticercus fasciolaris, 170

D
Dibothriocephalinae, 88
Dibothriorhynchus ruficollis, 51
Dibothrium, 17, 70, 88, 95, 153, 171
Dibothrium angustatum, 112
belones, 163
claviceps, 114
crassiceps, 154
hastatum, 71
heteropleurum, 159
infundibuliforme, 186
laciniatum, 133, 145, 147
ligula, 18, 19, 31
manubriforme, 133
microcephalum, 101
occidentale, 149
plicatum, 89, 136
proboscideum, 186
punctatum, 96
rugosum, 172
Dibothrius, 95, 153
Diphyllobothriidae, 11, 15, 93
Diphyllobothriinae, 42, 70
Diphyllobothrium, 70
Diphyllobothrium latum, 15, 42, 80, 199
Diplocotyle, 62
Diplocotyle cohaerens, 64
olrikii, 64
rudolphii, 56, 64
serrata, 64
Disymphytobothrium, 62
E
Echinococcifer, 14
Echinorhynchus, 53
Echinorhynchus xiphiae, 89
F
Fasciola, 17, 30
Fasciola abdominalis, 18
hepatica, 30
intestinalis, 18
Fimbriaria fasciolaris, 107
Fistulicola, 11, 88
Fistulicola plicatus, 11, 89
G
Gymnobothria, 9
H
Haematoloechus asper, 161
Halysis, 30
Halysis lanceolato nodosa, 31
Haplobothriinae, 11, 13, 15, 42, 70
Haplobothrium, 11, 13, 15, 43, 71, 93
Haplobothrium globuliforme, 7, 11, 15, 44, 74, 104, 160, 195
Hirudo, 30
Hirudo depressa alba, 30
L
Ligula, 17, 42
Ligula abdominalis, 18
abdominalis alburni, 18
abdominalis bramae, 18
abdominalis carassii, 18
abdominalis cobitidis, 18
abdominalis cyprinorum, 18
abdominalis gobionis, 18
abdominalis leucisci, 18
abdominalis trincae, 18
abdominalis vimbae, 18
acuminata, 18
alburni, 18
alternans, 19
avium, 18, 19
bramae, 18
carassii, 18
catostomi, 18
cingulum, 18
cobitidis, 18
colymbi, 18, 19
constringens, 18
contortrix, 18
crispa, 18
digramma, 18, 19
edulis, 18
gobionis, 18
interrupta, 19
intestinalis, 11, 17, 18, 19, 39
leucisci, 18
monogramma, 18, 19
nodosa, 19
petromyzontis, 18
piscium, 18
reptans, 19
salvelini, 18
simplicissima, 18, 19
sparsa, 19
trincae, 18
uniserialis, 19
vimbae, 18
Ligulinae, 11, 16, 70, 88
M
Marsipometra, 12, 16, 70, 93
Marsipometra hastata, 7, 12, 71
Marsipometrinae, 12, 15, 70
Monobothrium, 53
N
Nemertini, 51

P

Proteocephalus, 163
Pseudophyllidea, 13, 15, 118
Ptychobothriidae, 12, 15, 43, 70, 79, 93, 166
Ptychobothriinae, 12, 80, 94

R

Rhytelminthus, 81, 95
Rhytelminthus anguillae, 114
Rhytis, 30, 81, 95, 171
Rhytis bipunctata, 96
  claviceps, 114
  conoceps, 172
  salvelini, 186
  solida, 30

S

Schistocephalus, 8, 11, 17, 26, 30, 42, 137
Schistocephalus dimorphus, 9, 31
  gasterostei, 31
  nodosus, 31
  rhynchichthydis, 31
  solidus, 11, 24, 30, 31
  zschokkei, 31
Schistorhynchus dimorphus,
Scolex polymorphus, 133
Scyphocephalus, 16

T

Taenia, 17, 18, 30, 53, 81, 88, 95, 171
Taeniae, 105
Taenia acutissima, 30
  anguillae, 114
  capitata, 18
  capite truncato, 186
  cingulum, 18
  claviceps, 114
  crassa, 186
  decimpollicaris, 172
  gasterostei, 30, 31
  haeruca, 89
  lata, 30
  lanceolata nodosa, 31
  lanceolata var. β 31,
  nodularis, 31
  proboscidea, 186
  proboscis suilla, 186
  punctata, 96
  rugosa, 172
  salmonis, 186
  salvelini, 186
  scorpii, 96
  solida, 30
  tetragonoceps, 172, 186
  truncata, 57
Taenioidea, 51
Tetraphyllidea, 51
Tetrarhynchus, 51
Tetrarhynchus longicollis, 51
Triaenophorinae, 10, 11, 16, 45, 70, 81
Triaenophorus, 11, 42, 70, 81, 82
Triaenophorus nodulosus, 80, 82
  robustus, 82
Tricuspidaria, 81
Trypanorhyncha, 13, 42, 45

V

Vermis multimembris, 114
  multimembris rhombi, 96
Vesicaria, 81

ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. IV April, 1918 No. 4

NORTH AMERICAN PSEUDOPHYLLIDEAN CESTODES FROM FISHES

WITH THIRTEEN PLATES

BY

ARTHUR REUBEN COOPER

Price $2.00

PUBLISHED BY THE UNIVERSITY OF ILLINOIS
UNDER THE AUSPICES OF THE GRADUATE SCHOOL
URBANA ILLINOIS

UNIVERSITY OF ILLINOIS STUDIES PUBLISHED

ILLINOIS BIOLOGICAL MONOGRAPHS

THE ILLINOIS BIOLOGICAL MONOGRAPHS is a serial published quarterly by the University of Illinois. It is the purpose of the publication to present in monographic form research contributions of especial merit and of somewhat extended character. Each volume will include about 500 pages and 20 or more full page plates. The series may be obtained at a subscription price of three dollars yearly. Individual numbers will be sold separately at prices determined by the size and amount of illustration contained in the particular number.

Vol. I

Nos. 1 and 2. A Revision of the Cestode family Proteocephalidae. With 16 plates. By G. R. La Rue. $2.00.

No. 3. Studies on the Cestode family Anoplocephalidae. With 6 plates. By H. Douthitt. 80 cts.

No. 4. Some North American Larval Trematodes. With 8 plates. By W. W. Cort. $1.20.

Vol. II

No. 1. Classification of Lepidopterous larvae. With 10 plates. By S. B. Fracker. $1.50.

No. 2. On the Osteology of some of the Loricati. With 5 plates. By J. E. Gutherlet. 50 cts.

No. 3. Studies on Gregarines, including twenty-one new species and a synopsis of the Eugregarine records from the Myriapoda, Coleoptera, and Orthoptera of the world. With 15 plates. By Minnie E. Watson. $2.00.

No. 4. The Genus Meliola in Porto Rico. With 5 plates. By Frank L. Stevens. 75 cts.

Vol. III

No. 1. Studies on the factors controlling the rate of regeneration. By Charles Zeleny. $1.25.

No. 2. The head-capsule and mouth-parts of Diptera. With 25 plates. By Alvah Peterson. $2.00.

No. 3. Studies on North American Polystomidae, Aspidogastridae, and Paramphistomidae. With 11 plates. By Horace W. Stunkard. $1.25.

No. 4 Color and color-pattern mechanism of Tiger Beetles. With 29 black and 3 colored plates. By Victor E. Shelford. $2.00.

Vol. IV

No. 1. Life history studies on Montana Trematodes. By E. C. Faust. With 9 plates. $2.00.

No. 2. The Goldfish as a test animal in the study of toxicity By E. B. Powers. $1.00.

No. 3. Morphology and biology of some Turbellaria from the Mississippi basin. With 3 plates. By Ruth Higley. $1.25.

No. 4. North American pseudophyllidean Cestodes from fishes. With 13 plates. By A. R. Cooper. $2.00

Vol. V

No. 1. The Skull of Amiurus With 8 plates. By J. E. Kindred. (in press)

UNIVERSITY OF ILLINOIS STUDIES IN LANGUAGE AND LITERATURE

The Studies in Language and Literature are designed to include monographs in general linguistics and comparative literature; the classical languages and Sanskrit; the Romance languages; and English, the Scandinavian, and other Germanic languages. The title of the series will be so construed as to admit the publication of such researches in the history of culture as may throw light on the processes of language and the interpretation of literature. This series is published quarterly; the annual subscription price is three dollars.

Vol. I

Nos. 1 and 2. The phonology of the dialect of Aurland, Norway. By G. T. Flom. $1.25.

Nos. 3 and 4. Studies in the Milton tradition. By John Walter Good. $1.75.

Entered as second-class matter July 27, 1915, at the post-office at Urbana, Illinois, under the Act of August 24, 1912. Acceptance for mailing at the special rate of postage provided for in section 1103, Act of October 3, 1917, authorized July 31, 1918

UNIVERSITY OF ILLINOIS STUDIES IN LANGUAGE AND LITERATURE.—Continued.

Vol. II

No. 1. Thomas Warton: a biographical and critical study. By Clarissa Rinaker. $1.00.
No. 2. Illustrations of medieval romance on tiles from Chertsey Abbey. By Roger Sherman Loomis. 75 cts.
No. 3. Joseph Ritson: a critical biography. By Henry Alfred Burd. $1.15.
No. 4. Miscellanea Hibernica. By Kuno Meyer. $1.00.

Vol. III

No. 1. The *Ad Deum Vadit* of Jean Gerson. By David Hobart Carnahan. $1.75.
No. 2. Tagalog Texts with grammatical analysis. Part I. Texts and translation. By Leonard Bloomfield. $1.50.
No. 3. The same. Part II. Grammatical analysis. By Leonard Bloomfield. $3.00.
No. 4. The same. Part III. List of formations and glossary. By Leonard Bloomfield. $1.50.

Vol. IV

No. 1. Madame de Stael's literary reputation in England. By Robert C Whitford. 75 cts.
No. 2. Index verborum quae in Senecae fabulis necnon in Octavia Praetexta reperiuntur a Guilielmo Abbott Oldfather, Arthuro Stanley Pease, Howardo Vernon Canter confectus. (In press.)

UNIVERSITY OF ILLINOIS STUDIES IN THE SOCIAL SCIENCES

The University of Illinois Studies in the Social Sciences are designed to afford a means of publishing monographs prepared by graduate students or members of the faculty in the departments of history, economics, political science, and sociology. Each volume will consist of about 600 printed pages annually. The subscription price is three dollars a year.

Vol. I

Nos. 1 and 2. Financial history of Ohio. By E. L. Bogart. $1.80.
No. 3. Sources of municipal revenues in Illinois. By L. D. Upson. *Out of print.*
No. 4. Friedrich Gentz: an opponent of the French revolution and Napoleon. By P. F. Reiff. 80 cts.

Vol. II

No. 1. Taxation of corporations in Illinois, other than railroads, since 1872. By J. R Moore. 55 cts.
Nos. 2 and 3. The West in the diplomatic negotiations of the American Revolution. By P. C. Phillips. $1.25.
No. 4. The development of banking in Illinois, 1817–1863. By G. W. Dowrie. 90 cts.

Vol. III

Nos. 1 and 2. The history of the general property tax in Illinois. By R. M. Haig. $1.25.
No. 3. The Scandinavian element in the United States. By K. C. Babcock. *Out of print.*
No. 4. Church and state in Massachusetts, 1691–1740. By Susan M. Reed. $1.05.

Vol. IV

Nos. 1. The Illinois Whigs before 1846. By C. M. Thompson. 95 cts.
No. 2. The defeat of Varus and the German frontier policy of Augustus. By W. A. Oldfather and H. V. Canter. 75 cts.
Nos. 3 and 4. The history of the Illinois Central railway to 1870. By H. G. Brownson. $1.25.

Vol. V

No. 1. Enforcement of international law by municipal law in the United States. By Phillip Quincy Wright. $1.25.
No. 2. The life of Jesse W. Fell. By Frances M. Morehouse. 60 cts.
No. 3. Land tenure in the United States with special reverence to Illinois. By Charles L. Stewart. 75 cts.
No. 4. Mine taxation in the United States. By L. E. Young. $1.50.

Vol. VI

Nos. 1 and 2. The veto power of the Governor of Illinois. By N. H. Debel. $1.00.
No. 3. Wage bargaining on the vessels of the Great Lakes. By H. E. Hoagland. $1.50.
No. 4. The household of a Tudor nobleman. By P. V. B. Jones. $1.50.

UNIVERSITY STUDIES

GENERAL SERIES, Vol. I, II, AND III
Partly out of print. A detailed list of these numbers will be sent on request.

Vol. IV

No. 1. The origin of the land grant of 1862 (the so-called Morrill act) and some account of its author, Jonathan B. Turner. By E. J. James. Cloth $1.35; paper 75 cts.
No. 2. Fragment RA.58C of Konongs Skuggsja, from an old Norwegian parchment codex of the XIIIth century, with heliotype copy and a study of the pal ‹ graphy and the language. By G. T. Flom. $1.25.
No. 3. Michel-Jean Sedaine: Le philosophe sans le scavoir. Variorum critical edition, based upon the second Paris edition of 1766 and its appendix with an introduction treating of all known editions and translations. By T. E. Oliver. $1.75.

PUBLICATIONS OF THE UNIVERSITY OF ILLINOIS

Following is a partial list of the publications issued at the University:

1. THE UNIVERSITY OF ILLINOIS STUDIES IN LANGUAGE AND LITERATURE. Published quarterly. Three dollars a year.

2. THE UNIVERSITY OF ILLINOIS STUDIES IN THE SOCIAL SCIENCES. Monographs in history, economics, political science, and sociology. Quarterly. Three dollars a year.

3. THE ILLINOIS BIOLOGICAL MONOGRAPHS. Quarterly. Three dollars a year.

4. THE UNIVERSITY STUDIES. A series of monographs on miscellaneous subjects.

5. THE JOURNAL OF ENGLISH AND GERMANIC PHILOLOGY. Quarterly. Three dollars a year.

For any of the above address 156 Administration Building, Urbana, Illinois.

6. THE BULLETIN OF THE ENGINEERING EXPERIMENT STATION. Reports of thee research work in the Engineering Experiment Station. Address Director of Engineering Experiment Station, University of Illinois.

7. THE BULLETIN OF THE AGRICULTURAL EXPERIMENT STATION. Address Director of Agricultural Experiment Station, University of Illinois.

8. THE BULLETIN OF THE STATE LABORATORY OF NATURAL HISTORY. Address Director of State Laboratory of Natural History, University of Illinois.

9. THE BULLETIN OF THE STATE GEOLOGICAL SURVEY. Address Director of State Geological Survey, University of Illinois.

10. THE BULLETIN OF THE STATE WATER SURVEY. Address Director of State Water Survey, University of Illinois.

11. THE REPORT OF THE STATE ENTOMOLOGIST. Address State Entomologist, University of Illinois.

12. THE BULLETIN OF THE ILLINOIS ASSOCIATION OF TEACHERS OF ENGLISH. Address 301 University Hall, University of Illinois.

13. THE BULLETIN OF THE SCHOOL OF EDUCATION. Address 203 University Hall, University of Illinois.

14. THE LAW BULLETIN. Address 207 Law Building, University of Illinois.

15. The general series, containing the University catalog and circulars of special departments. Address The Registrar, University of Illinois.